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SOME ASPECTS OF THE MORPHOLOGY OF THE INSECT HEAD AS SEEN IN THE LEPIDOPTERA.

By J. R. T. Short, B.Sc., F.R.E.S.

(*Hope Department of Entomology, University of Oxford.*)

A. Introduction.

The purpose of this paper is to discuss several aspects of head morphology which may be studied in the Lepidoptera. These are :

1. Are Snodgrass' criteria for the identification of the frons and clypeus of insects valid for the head of caterpillars ?
2. What are the morphological differences between the head of the larval and the head of the adult Sphingid ? How are these structural differences related to function ?
3. What is the "ocular diaphragm" which Ferris (1942) claims to have discovered in the insect head ?

The terminology used is, unless otherwise stated, that of Snodgrass. Kloet and Hincks (1945) have been followed in nomenclature.

B. Terminology.

1. On Sutures.

It has been usual to describe the insect cranium as being marked off into "sclerites" by "sutures." This word "suture" included a variety of structures. Du Porte (1946) and Snodgrass (1947) have proposed new terms for some of the structures formerly grouped under "suture." The following terms have been adopted from Snodgrass :

Suture.—This is a line of union between separate areas of dermal hardening. An example is the suture between the hypostomal lobes of the head of the larval *Dilina tiliae* (L.) (see figs. 8, 9, *y*).

Ecdysial cleavage line.—This is a line of weakness in the head cuticle which will split at ecdysis (Henriksen, 1932 ; Frankenberg, 1940). Along such a line the exocuticle is wanting and the endocuticle extends up to the epicuticle (Wigglesworth, 1948). The "epicranial suture" of nymphs and larvae is an ecdysial cleavage line. The word epicranial will not be used, but the words coronal and frontal will be retained in the sense of the coronal stem and the frontal arms of the ecdysial cleavage line. Hinton (1947) has noted the occurrence of cleavage lines on the ventral surface of the heads of many larvae, e.g., some Megaloptera, Coleoptera, Trichoptera and a few Lepidoptera (some Hesperiidae). The ecdysial cleavage lines may therefore be differentiated as dorsal and ventral.

Sulcus.—This is an external groove marking an infolding of the cuticle to form an endoskeletal strengthening ridge or apodeme. Most of the structures formerly called head sutures are of this type.

There is a fourth class of structure to which a new name has not been given. Snodgrass (1935 : 53) has distinguished this class as "lines where the sclerotization of the cuticle has become secondarily discontinuous in order to give flexibility." He does not give an example, but I believe that the line between the clypeus and labrum and the lines between the podomeres of the appendages are of this nature. These lines permit movement of sclerotized parts.

Snodgrass' definition of this class of structure is based on its probable origin in evolution. This does not give a ready basis for identification. These structures are here called articular lines (fig. 6, *a.l.*). The membrane (fig. 10, *a.m.*) which allows movement of a sclerotized area or areas is called an articular membrane.

Articular lines and sutures are similar in structure; but they differ in function as well as in origin. A suture does not allow movement between sclerotized parts.

On the insect cranium are further lines which do not come under the four groups listed above. For example, in the larvae of the Hymenoptera-Apocrita there are cranial grooves above the developing imaginal eyes. These grooves differ from sulci in that they are not obviously strengthening the cranium against distortion due to muscular contractions.

2. On the Definition of Cranial Areas.

Snodgrass' (1947) revision of the term "suture" has also affected his definition of the limits of the frontal area. It is necessary to consider the remaining cranial areas with reference to this revision.

A suture occurs by the union of two identical cranial areas. It can therefore indicate only the line between these areas of sclerotization (see figs. 8, 9, *y*).

The frontal arms of the dorsal ecdysial cleavage line (fig. 1, *d.e.c.l.*) were previously held to be the dorso-lateral limits of the frons (*fr.*). These arms have been shown (Snodgrass, 1947) to differ in position in different groups of insects. The term frons can now be used only in an indefinite sense for the facial area of the head above the clypeus (*clp.*). The only part of the frons which can be definitely recognized is that on which its muscles have origin (see section C of this paper). It follows that there is no exact boundary between the frons and the parietals (fig. 6, *p*).

The cranial areas are still defined mainly by the sulci present in the Orthopteroid head. All of these sulci are not present in other insects. For example, when the occipital sulcus is absent, there is no line between the parietals and the occipital area (fig. 12, *p*, *o.*).

In most insects the labrum is marked off from the clypeus by an articular line.

3. On the Apotome.

The facial area cut out by the splitting of the dorsal ecdysial cleavage lines is called the apotome. The cleavage lines may take five different facial positions. At one extreme they go to the compound eyes; at the other they go mesad of the antennae to the distal margin of the clypeus. Snodgrass (1947: 46) states that the frons is usually cut into three sections by the frontal arms of the cleavage line. If the arms extend through the clypeus, this is cut in the same manner. The apotome may thus be the median part of the frons (frontal apotome) or the median parts of the frons and clypeus (frontoclypeal apotome). The apotome of caterpillars consists of the median part of the frons and the entire clypeus. Snodgrass refers to this also as a frontoclypeal apotome.

One feature of this interpretation of the apotome needs further explanation. The frons is an indefinite area. Yet it is claimed that the frontal arms of the cleavage line divide the frons into three parts. It is assumed that the grounds for this claim are as follows. The cleavage lines usually separate the region of the cranium on which the mandibular muscles arise from that on which the facial (frontal and clypeal) muscles arise. Therefore, part of the area between the cleavage lines can be definitely identified as the frons. But the arms of the cleavage line vary in position. Some indefinite part of the frons must be considered to lie outside the cleavage lines.

c. On the Frons and Clypeus of Caterpillars.

Snodgrass (1928, 1935, 1947) claims that the frons and clypeus of the caterpillar head can be recognized by the criteria which he has established from a study of generalized insects. These criteria may be summarized as follows (see Snodgrass, 1935, fig. 155) :

Clypeus.—The dorsal (posterior) limit of the clypeus is the epistomal sulcus. The basal angles of the clypeus carry the anterior mandibular articulations. The lateral limits are obvious, since the clypeus is part of a pre-oral lobe in generalized insects. The ventral (anterior) limit is the articular line (formerly called the clypeo-labral suture) between the clypeus and the labrum.

The muscles which have origin on the clypeus are the cibarial muscles and the dorsal muscles of the buccal cavity (that part of the stomodaeum which lies just within the mouth).

The insertion of the clypeal muscles is ventral (anterior) to the frontal ganglion.

Frons.—The ventral (anterior) limit of the frons is the epistomal sulcus. There are no dorso-lateral limits, since the position of the frontal arms of the cleavage line differs in different groups of insects.

The muscles which have origin on the frons are the labral, precerebral pharyngeal and hypopharyngeal muscles.

The insertion of the precerebral muscles is dorsal (posterior) to the frontal ganglion. The precerebral pharyngeal and hypopharyngeal muscles are encircled by the frontal ganglion connectives.

The epistomal sulcus.—This sulcus usually contains the anterior tentorial pits.

Using these criteria, Snodgrass interprets the triangular plate on the anterior surface of the caterpillar head as the clypeus (fig. 1, *clp.*). That part of the frons (*fr.*) which lies between the arms of the dorsal ecdysial cleavage line *d.e.c.l.*) has the form of an inverted Y. The stem of this Y is invaginated into the head, and the arms are the regions often called the " adfrontals " (fig. 3, *a.a.*). The epistomal sulcus (fig. 1, *e.s.*) is sharply arched, but may be recognized for its ridge (fig. 7, *e.r.*) bears the anterior tentorial arms (*a.t.a.*). Only the frontal arms of the cleavage line are present. These lines are closely approximated along the sides of the narrow invaginated part of the frons. Below this they diverge, running along the sides of the " adfrontal areas " to the anterior mandibular articulations (fig. 10, *a.m.a*).

Hinton (1947) has directed attention to the fact that two pairs of the precerebral pharyngeal muscles of caterpillars do not arise on the frons. The position of these muscles thus conflicts with Snodgrass' criteria listed above. One pair of muscles (figs. 4, 5, No. 3) arises laterad of the cleavage lines near the place of origin of the antennal retractors (*r.a.*). Another pair (No. 1) arises on the clypeus. This disposition of muscles has been found by Hinton in several distantly related caterpillars: Yponomeutidae (*Yponomeuta*), Geometridae (undet.), Caradrinidae (*Polia nebulosa* (Hufn.)), and Lasiocampidae (*Poecilocampa populi* (L.)). He is therefore unwilling to accept Snodgrass' interpretation of the caterpillar head.

Hinton substitutes an interpretation (fig. 3) of the caterpillar head in which the external grooves of the external Y-shaped ridge are called the " adfrontal sutures." The stem of the Y-shaped ridge is a mid-cranial sulcus marked externally by the " median adfrontal suture " (*m.a.s.*). The anterior arms of the median adfrontal suture are the " lateral adfrontal sutures " (*l.a.s.*). The cranial areas between the " adfrontal " and " epicranial sutures " are the " adfrontal areas " (*a.a.*). The frontal and clypeal areas are not differentiated. Since Hinton refers to " the fronto-clypeal apotome," I assume that he considers the region bounded by the cleavage lines to be a frontoclypeal area in which it is not possible to distinguish frons and clypeus. Hinton does not identify the triangular plate on the anterior surface of the head as the clypeus. He believes it to be merely part of the frontoclypeal apotome.

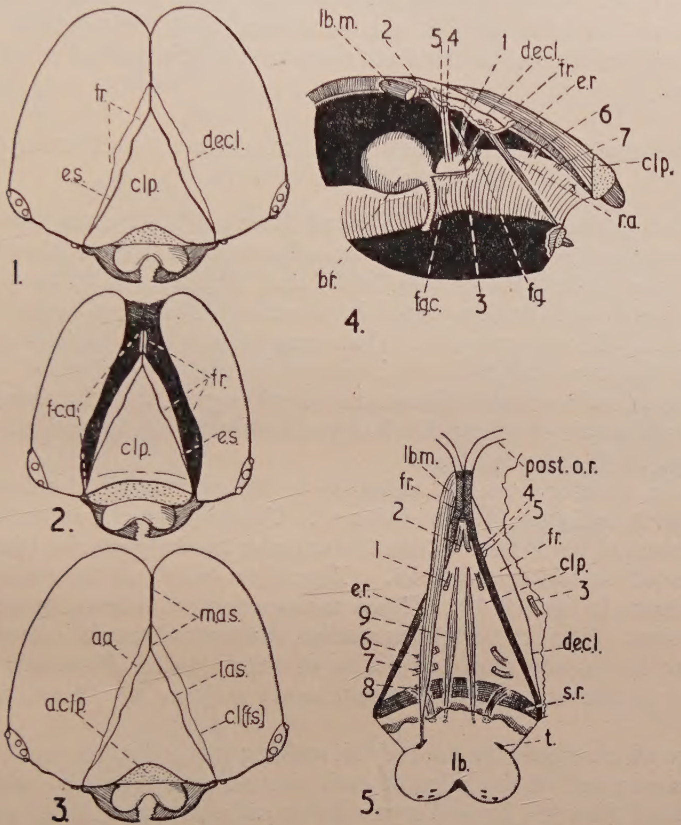
In an attempt to clarify this position, the heads of the following caterpillars have been studied: Caradrinidae (*Brachionycha sphinx* (Hufn.), *Eupsilia transversa* (Hufn.)), Selidosemidae (*Ourapteryx sambucaria* (L.)), Cossidae (*Cossus cossus* (L.)), Papilionidae (*Papilio machaon* L.), Sphingidae (*Dilina tiliae* (L.)), Hypsidae (*Panaxia dominula* (L.)), Lasiocampidae (*Lasiocampa quercus* (L.)). There was little variation in head structure between these species.

The positions of the facial muscles of these caterpillars agree completely with Hinton's findings. They do not agree with Snodgrass' (1947 : 34) statement that: " . . . , the postganglionic muscles, or precerebral dilators of the pharyngeal region of the stomodaeum, take their origins on the narrow strips between the cleavage lines and the apex of the clypeal triangle. . . ." It is this statement which has been criticized by Hinton. However, the positions of the facial muscles do agree with Snodgrass' description of 1928. Controversy centres on the positions of the precerebral pharyngeal muscles which I have numbered 1 and 3 (see figs. 4, 5). These only need be described.

Muscle pair No. 1 has origin on the clypeus. These muscles are numbered 24 by Snodgrass (1928). He records that they arise on the upper part of the clypeus, and suggests that they have crossed the epistomal ridge to reach this point.

Muscle pair No. 3 has origin on the cranial walls laterad of the frontal arms of the dorsal ecdysial cleavage lines. These muscles are numbered 26 by Snodgrass. He state that they arise on the cranial walls laterad of the origin of the antennal muscles (*r.a.*). The antennal muscles are recorded as arising on the parietal walls of the cranium laterad of the " adfrontal areas." Snodgrass is clearly aware of the precise positions of origin of this pair of pharyngeal muscles. In the forms examined for this paper, pair No. 3 arises mesad of the origin of the antennal retractors, not laterad as described by Snodgrass. This is not significant to the matter under discussion.

Snodgrass (1928) does not comment on the fact that two pairs of the precerebral pharyngeal muscles do not arise on what he identifies as the frons. Apparently the evidence of the remainder of the muscles, the epistomal sulcus and the anterior tentorial arms is held to outweigh these discrepancies. Thus he suggests that muscle pair No. 1 (in my description) has migrated.



Figs. 1–5.—Head of *Ourapteryx sambucaria* (L.) (Selidosemidae). (1) Anterior view of head labelled with terminology of Snodgrass. (2) Anterior view of exuviae. (3) Anterior view labelled with terminology of Hinton. (4) Lateral view of dissection showing precerebral pharyngeal and antennal muscles. (5) Internal view of median dorsal part of cranium dissected to show precerebral pharyngeal, cibarial and labral muscles.

The question raised by this work is whether these muscle discrepancies of the caterpillar head vitiate Snodgrass' method of recognizing the frons and clypeus of insects. It should be remembered that work exists which claims that Snodgrass' views on the arrangement of the facial muscles are substantially correct (see Dorsey, 1943 ; Cook, 1944). The present author has found that the positions of the facial muscles of the larvae of Hymenoptera agree with Snodgrass' generalization. Also Snodgrass' terms are applicable throughout all insect orders. Hinton's terminology is applicable only within the narrow limits of an order. Clearly, a large number of detailed investigations are needed before Snodgrass' criteria can be fully accepted or rejected. Du Porte's (1946 : 401) statement, " The known inconsistency of muscle origins throws doubt on their value in determining the homologies of the facial sclerites," expresses an extreme view. It seems more reasonable to retain Snodgrass' terminology for the caterpillar head until it can be shown that, in insects as a whole, numerous and widespread aberrations make invalid his method of establishing homologies.

D. ON THE CORRELATION BETWEEN SKELETAL FORM AND FUNCTION IN THE SPHINGID *Dilina tiliae* (L.).

Snodgrass (1928, 1932, 1935, 1947) and Strenger (1942) state that the sulci of the insect cranium mark the position of endoskeletal strengthening ridges. Also Snodgrass (1928, 1932, 1935, 1947) and Wheeler (1927) have observed that the cranial parts are developed in accordance with the size of the major head muscles. These two related ideas may be examined by comparing the cranium of the larva of *D. tiliae* with that of the adult.

There are no adequate studies on the morphology of the adult head. Snodgrass' criteria have been followed in interpreting the frons, clypeus and epistomal sulcus (figs. 12–17, *fr.*, *clp.*, *e.s.*).

The sulci running from the antennae to the post-occipital sulcus may be called postantennal sulci (fig. 12, *post a.s.*). The sulci which run on the ventro-lateral surface of the cranium from the anterior to the posterior tentorial pits may be called ventral cranial sulci. (The ridges (*v.c.r.*) of the ventral cranial sulci are shown in figs. 13–16). These names are given merely for convenience in description. Schmitt (1938) has studied the ventral cranial sulcus and considers that it consists morphologically of three parts. However, from the standpoint of function the three components may be considered as a single sulcus.

A ridge which braces the floor of the sucking pump (fig. 16, *s.p.*) is attached to the anterior end of the ridge of each ventral cranial sulcus. Schmitt has demonstrated that the hypopharynx forms at least the anterior part of the floor of the sucking pump. These ridges of the sucking pump may therefore be called hypopharyngeal ridges (figs. 13, 16, *hp.r.*).

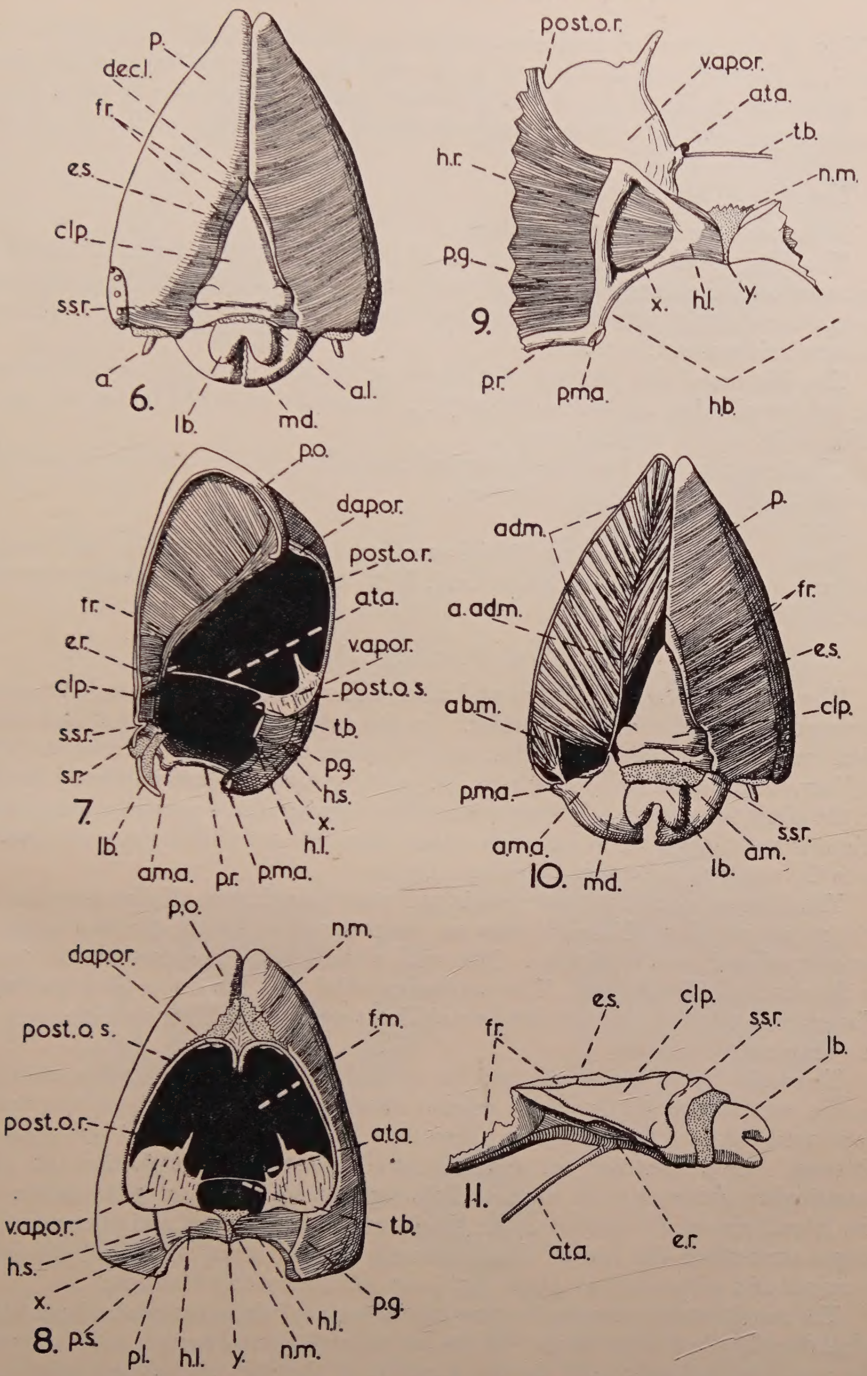
1. Muscles.

Only the major cranial muscles will be described.

a. The Larva (figs. 6–10).

Each abductor muscle of the mandible (*ab.m.*) is a relatively small group of fibres having origin on the lateral part of the ventral apodeme of the post-occipital ridge (*v.a.p.o.r.*). Insertion is on a small apodeme extending from the lateral aspect of the mandible.

Each adductor muscle of the mandible (*ad.m.*) is a huge group of fibres



FIGS. 6–11.—Head of larval *Dilina tiliae* (L.) (SPHINGIDAE). (6) Anterior view. (7) Head capsule dissected to show internal structures. (8) Posterior view of head capsule. (9) Internal view of hypostomal bridge and associated structures. (10) Internal view of dissection showing mandibular muscles. (11) Frontoclypeal apotome.

arising on the anterior, posterior, dorsal and lateral cranial walls above the ocelli, on the mid-cranial ridge and on the ventral apodeme of the post-occipital ridge mesad of the origin of the abductor muscles. Insertion is on a large apodeme (*a.adm.*) extending dorsally from the medial aspect of the mandible.

b. The Adult (figs. 12–17).

Muscles of the sucking pump (*s.p.*) :—

The dilators of the cibarium (*d.c.*1, 2 and 3) are three groups of muscles inserting on the anterior and dorsal walls of the sucking pump. The first two groups have origin on the clypeus (*clp.*), and the third on the epistomal and antennal ridges (*e.r.*, *a.r.*).

The dilators of the pharynx (*d.p.*) have origin on the median component of the epistomal ridge and on the frons (*fr.*). Insertion is on the dorsal and posterior walls of the sucking pump.

(The buccal cavity forms some part of the sucking pump, but it is impossible to distinguish its precise contribution).

Antennal muscles :—

Arising on each anterior tentorial arm (*a.t.a.*) and inserting on each scape (*sc.*) are a pair of levator muscles (*l.a.*1, *l.a.*2) and a pair of depressor muscles (*d.a.*1, *d.a.*2.).

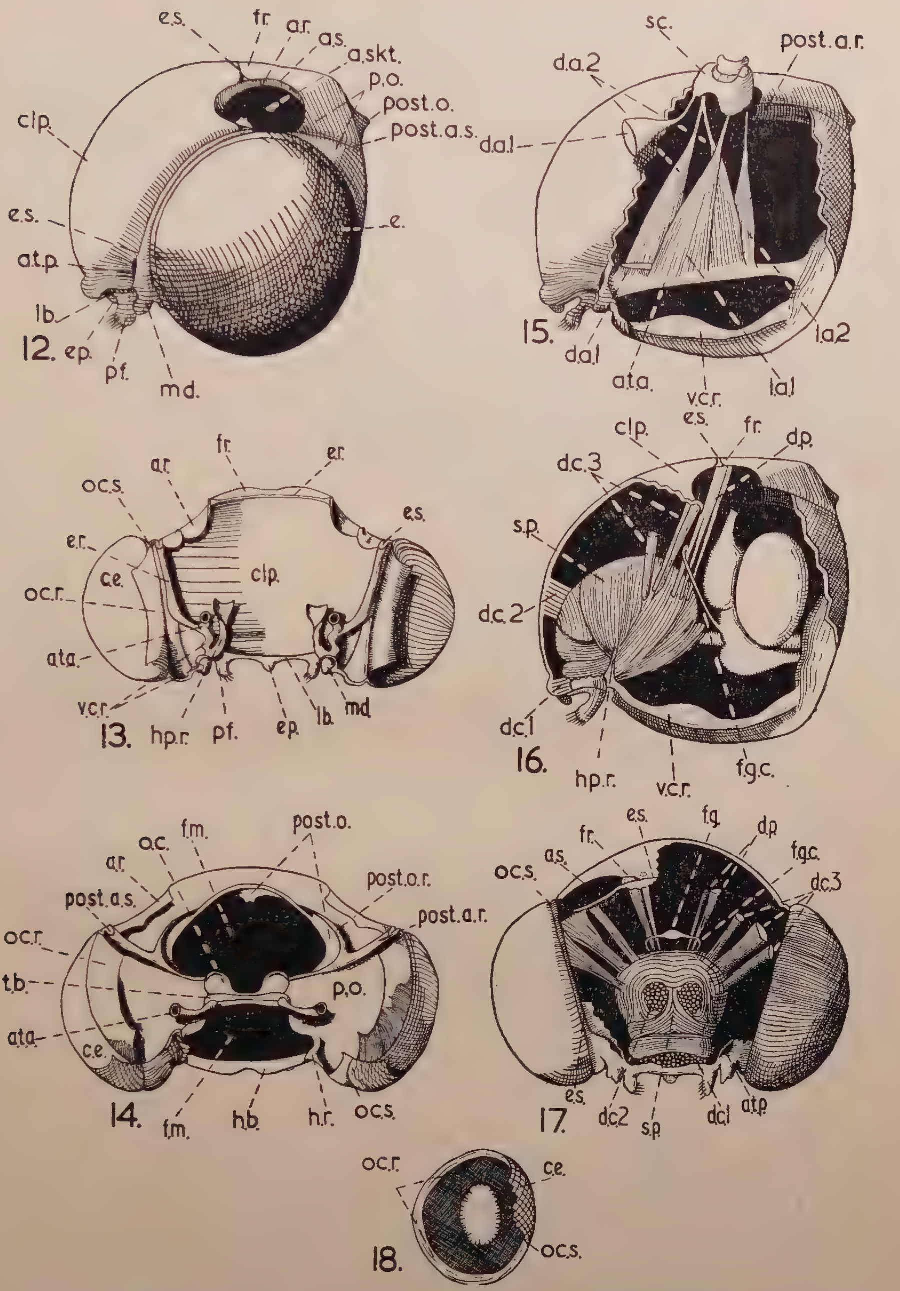
2. Skeletal Form and Function.

The cranial areas of the larva and adult differ in extent. These differences correspond with the feeding muscles. In the caterpillar the parietal and occipital cranial areas (figs. 6, 7, 8, *p.*, *p.o.*) whereon the mandibular muscles (fig. 10) have origin are huge. The frons (*fr.*) and clypeus (*clp.*) are relatively small. In the adult the clypeus whereon most of the muscles of the sucking pump have origin is very large. The parietals, other than the compound eyes, are small, as is the occipital area (fig. 12, *p*, *o.*, *e.*).

The tubular exoskeleton of insects will resist bending in all directions, as it will resist twisting. There is also an economy in material, for the neutral zone is reduced to a minimum. But with a thin, plate-like exoskeleton there is the danger of buckling. This applies especially to the dome-like cranium. The cranial sulci (and ridges) act as stabilizers against buckling or distortion of the cranium.

The main forces which will tend to cause buckling of the cranium are due to the contraction of the main cranial muscles. The function of the well-developed parts of the epistomal ridge (fig. 13, *e.r.*) of the adult Sphingid is obvious. As a contrast, in mandibulate insects the contraction of the mandibular adductor pulls the mandible against its points of articulation on the lateral rim of the cranium. In the locust, the epistomal and pleurostomal ridges strengthen the rim of the cranium. In the larval Sphingid the submarginal and pleurostomal ridges (fig. 7, *s.r.*, *p.r.*) have this function.

The cranial area between the two lateral parts of the epistomal ridge of the adult has the form of an arch. In the larva, each lateral cranial area between the post-occipital ridge and the combination of the mid-cranial and epistomal ridges has the form of an arch (figs. 6, 7, 8). The contraction of the muscles which are attached to an arch causes lateral thrusts which are resisted by the ridges. The ridges thus act as the “ abutments ” of the arch.



FIGS. 12–18.—Head of adult *Dilina tiliae* (L.) (SPHINGIDAE). (12) Dorso-lateral view of cranium. (13) Internal view of anterior half of head capsule; the sucking pump has been dissected away to show the hypopharyngeal ridges. (14) Internal view of posterior half of head capsule. (15) Lateral view of dissection showing antennal muscles. (16) Lateral view of dissection showing precerebral pharyngeal and cibarial muscles. (17) Anterior view of dissection showing precerebral pharyngeal and cibarial muscles. (18) Skeleton of compound eye dissected to show ocular ridge.

The tentorium often serves for muscle attachment, but it also braces the cranium against distortion. In caterpillars, the tentorium (figs. 7, 8) is absent or weakly developed. The mid-cranial and epistomal ridges (fig. 7) prevent cranial distortion. The origin of the hypostomal bridge (fig. 9, *h.b.*) of caterpillars is perhaps connected with the poorly developed tentorial bar. As a contrast, the tentorium of the adult Sphingid is well developed with powerful antennal muscles arising on the anterior arms (fig. 15).

E. ON THE "OCULAR DIAPHRAGM" OF FERRIS.

Ferris (1942 : 40) has discovered an "area beneath the bulging eye" which he calls the "ocular diaphragm." It is usually deeply pigmented. This "diaphragm" is clearly the ridge (figs. 13, 14, 18, *oc.r.*) of the ocular sulcus (*oc.s.*) of the compound eye (fig. 12, *e.*) (see Snodgrass (1935). The condition is well illustrated in the adult of *D. tiliae.*

F. ACKNOWLEDGMENTS.

This work was carried out under the supervision of Professor G. C. Varley, to whom I am indebted for much kind help. I also wish to thank Dr. H. E. Hinton, who discussed the terminology of the caterpillar head with me, and Mr. H. E. Smith, who has advised me on several points of structural mechanics.

G. SUMMARY.

1. Hinton's (1947) criticisms of Snodgrass' views on the frons and clypeus of the caterpillar head are examined. Both authors are shown to be in agreement on facts. The importance of the deviations from Snodgrass' generalizations which occur in the caterpillar head cannot be estimated without further detailed studies into other groups. Present evidence indicates that these generalizations are substantially correct. His terminology, which is based on the belief that it is possible to establish homologies between the orders of insects, is therefore preferable to that of Hinton. The latter is applicable only within the Lepidoptera.

2. The cranium and major head muscles of the larva and adult of the Sphingid *D. tiliae* have been compared. It has been shown that :—

(*a*) The cranial areas differ in extent in accordance with the development of the muscles inserted thereon. The occipito-parietal areas and the mandibular muscles are dominant in the larval head. The clypeus and the cibarial muscles are dominant in the head of the adult.

(*b*) Cranial sulci are the external manifestations of internal ridges which strengthen the cranial walls. The manner in which these ridges strengthen the cranium is examined.

3. The "ocular diaphragm" of Ferris (1942) is shown to be the ridge of the ocular sulcus of Snodgrass (1935).

ABBREVIATIONS USED ON THE FIGURES.

a., antenna.
a.a., adfrontal area of Hinton.
a.clp., anteclypeus of Hinton.
ab.m., abductor of mandible.
ad.m., adductor of mandible.
a.ad.m., apodeme of adductor of mandible.
a.l., articular line.
a.m., articular membrane.
a.m.a., anterior mandibular articulation.
a.r., antennal ridge.
a.s., antennal sulcus.
a.skt., antennal socket.
a.t.a., anterior tentorial arm.
a.t.p., anterior tentorial pit.
br., brain.
c.e., cornea of eye.
c.l.(*f.s.*) cleavage line (frontal suture) of Hinton.
clp., clypeus.
*d.a.*1., first depressor of antenna.
*d.a.*2., second depressor of antenna
d.a.p.o.r., dorsal apodeme of postoccipital ridge.
*d.c.*1., first dilator of cibarium.
*d.c.*2., second dilator of cibarium.
*d.c.*3., third dilator of cibarium.
d.e.c.l., dorsal ecdysial cleavage line.
d.p., dilators of pharynx.
e., compound eye.
ep., epipharynx.
e.r., epistomal ridge.
f-c.a., frontoclypeal apotome.
f.g., frontal ganglion.
f.g.c., frontal ganglion connectives.
f.m., foramen magnum.
fr., frons.
h.b., hypostomal bridge.
h.l., hypostomal lobe.
h.r., hypostomal ridge. In the adult Sphingid, this is part of the ventral cranial ridge.
h.s., hypostomal sulcus.
hp.r., hypopharyngeal ridge.
*l.a.*1., first levator of antenna.
*l.a.*2., second levator of antenna.
l.a.s., lateral adfrontal suture of Hinton.
lb., labrum.
lb.m., labral muscle.
m.a.s., median adfrontal suture of Hinton.
md., mandible.
n.m., neck membrane.
o.c., occipital condyle.
oc.r., ocular ridge.
oc.s., ocular sulcus.
p., parietal region of cranium.
pf., pilifer.
p.g., postgenal region of cranium.
pl., pleurostoma.
p.m.a., posterior mandibular articulation.
p.o., parietal and occipital regions of cranium.
post.a.r., postantennal ridge.
post.a.s., postantennal sulcus.
post.o., postocciput.
post.o.r., postoccipital ridge.
post.o.s., postoccipital sulcus.
p.r., pleurostomal ridge.
p.s., pleurostomal sulcus.
p.t.p., posterior tentorial pit.
r.a., retractor of antenna.
sc., scape of antenna.
s.p., sucking pump.
s.r., submarginal ridge of clypeus.
s.s.r., sulcus of submarginal ridge of clypeus.
t., torma.
t.b., tentorial bar.
v.c.r., ventral cranial ridge.
v.a.p.o.r., ventral apodeme of postoccipital ridge.
x., sulcus and ridge of ventral margin of hypostomal lobe.
y., suture between the hypostomal lobes.
1–5, precerebral pharyngeal muscles of caterpillar.
6–9, cibarial muscles of caterpillar.

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BOOK NOTICE.

The chemistry and action of insecticides. By HAROLD H. SHEPARD. 8vo. London and New York (McGraw-Hill), 1951. Pp. vii + 504, 18 figs. Price 59*s.* 6*d.*

Written from the chemist's, not the entomologist's viewpoint, this work classifies the insecticides according to their chemical relationships, and is set out like a text-book of chemistry. At the same time it is intended for the practical entomologist, and is intended to be intelligible to anyone with a little basic knowledge of inorganic and organic chemistry. Two later chapters deal with the general aspects of chemical control of insects, and with the relative toxicity and mode of application of insecticides.

An appendix gives tables of chemical and physical constants, specific gravity, temperature, humidity, and such useful data as the compatibility of common spray materials, and the explosive limits of mixtures of some inflammable liquids and gases with air.

THE STRIDULATION OF *EREMOGRYLLUS HAMMADAE* KRAUSS (ORTHOPTERA, ACRIDIDAE).

By E. S. Brown, B.A., F.R.E.S.

While travelling on the Jebel, a mountain range in north Tripolitania some 50 miles from the coast, the writer had a surprising experience near Nalut on 24th April, 1946.

Stridulation among Acrididae was rare in the territory at this time, and the sound of what appeared to be two or three different species stridulating on sandy ground, at an altitude of 600 metres, was therefore arresting. A thorough search, however, revealed only one species, and on watching it through field glasses it was found to be alone responsible for all the different sounds, which it produced in an apparently regular sequence.

Specimens captured were subsequently identified by Dr. B. P. Uvarov as *Eremogryllus hammadae* Krauss, a species recorded hitherto from Morocco, southern Algeria, Tunisia and Tripolitania. I am grateful to him for his identification, and for calling attention to a paper[1] in which Volkonsky describes the stridulation of this grasshopper. Since my own observations are not completely in accordance with his, and since more was learned of the mechanism by which the insect produces and varies the pitch of the stridulation, this note has been prepared to place the facts on record. Notes were taken in the field of the three distinct sounds which the insect was observed to make, and are reproduced below.

(1) A high-pitched, shrill, piercing sound, audible at a considerable distance : duration 2 seconds.

(2) A series of low-pitched, short sounds, with a frequency of about two per second. Duration of whole series variable.

(3) A faint, scarcely audible, squeaky noise : duration 1–2 seconds.

These sounds are generally produced, one following immediately on the other, in the sequence 1–2–3, which may be repeated several times ; it may then be followed by 1–2–2–2–2–2–, the second series repeated an indefinite number of times. Volkonsky described only two noises, having possibly overlooked the faint sound (3) ; of his two, one is " low and loud," the other " higher and less loud," doubtless corresponding to (2) and (1) respectively, but the sequence he gives differs from that described above, and on the Jebel the higher sound could hardly be described as " less loud."

On other occasions in late March and April, 1946, *Eremogryllus hammadae* was found in the coastal plain between the Jebel and the sea (at Castel Benito, Castel Verde, Suani ben Adem, Tarhuna, El Azizia, and in the suburbs of Tripoli itself), and appears to have a wide distribution in these parts. Being an inconspicuous insect it was always detected through its stridulation, and although the stridulation was remarkable owing to the production of more than one type of sound, on no occasion was a performance witnessed which agreed at all closely with that in the Nalut colony. Notes were made in the field at Ain Zara (on the outskirts of Tripoli) on 24th March; the sounds were repeated at the rate of about 6 or 7 in five seconds, or rather more than one per second, with scarcely any gap between; each started with a high-pitched, shrill note, and finished with a low note, so that the performance strongly recalled the winding of a watch. The shrill note and the low one seem to correspond to sounds (1) and (2) respectively of the Nalut insects, but the duration and pattern of the stridulation was entirely different. There is, however, a greater similarity to the type of stridulation described by Volkonsky, in that high and low notes alternated regularly, but whereas each separate noise started on the high note and finished on the low one in the Tripoli locality, it was the reverse in Volkonsky's experience; he records also a very much slower frequency of repetition. It thus seems that there are three distinct stridulation patterns in *Eremogryllus hammadae*, which are compared diagrammatically in Fig. 1.

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[1] Uvarov, B. P., and Volkonsky, M. A., 1939, Notes on a desert grasshopper with digging habits, *Eremogryllus hammadae* Krauss, 1902 (Orthoptera, Acrididae). *Proc. R. ent. Soc. Lond.* (A) **14** : 19–23.

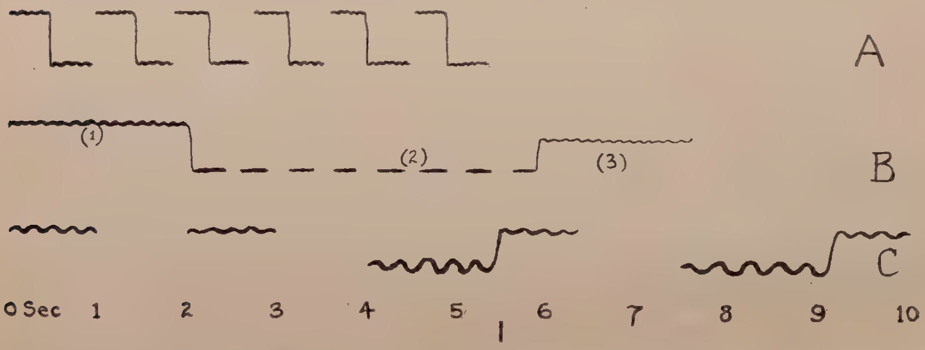


Fig. 1.—Stridulation of *Eremogryllus hammadae*. Height above base-line represents the pitch. A, type observed at Tripoli; B, at Nalut; C, stridulation as represented by Volkonsky. (1), (2), (3), sounds as described and numbered in the text.

Volkonsky failed to observe how the pitch of the sound was varied, and his only observation on the mechanism of stridulation was that the low-pitched sound was "accompanied by strong and wide vibration of half-opened elytra and wings." I have no note of any activity of this kind, although stridulating insects were clearly seen and watched both at Nalut and Tripoli. Volkonsky states that the insects were sunk into pits which they had excavated, and this would make observation more difficult, but no such procedure was observed on the occasions recorded here. Both at Tripoli and Nalut the noise was found to be produced by the common Acridid method of rubbing the hind femora against the elytra. Variation in pitch was accompanied by, and possibly produced by, change in the arc through which the hind femora vibrated as they rubbed the elytra. At Nalut, during the first, high-pitched noise (1) they were raised high and rotated through a wide angle, and for the low-pitched sound (2) through a smaller angle at a lower elevation (almost horizontal); the third, squeaky sound was made with the femora again raised, but not as high as in (1). These arcs of vibration are illustrated in fig. 2, which is based on a sketch made in the field. The sound (3) was very probably overlooked by Volkonsky because it is very faint and easily missed unless one can see the femora working and therefore be expecting it. An insect observed at Tripoli was also observed to raise the hind femora much higher during the shrill note than during the low one, although no precise note was made of their arc of vibration.

Microscopic examination of the stridulatory file on the inner face of the hind femur shows it to be relatively very long (nearly 4 mm., or just over half the length of the femur) and made up of closely spaced teeth. It will be readily seen from fig. 2 that when the femora are raised high, the more proximal parts of the comb and of the ridge on the elytron will engage, while if they are lowered it is the more distal parts which will engage. It is admittedly difficult to see how this in itself would create differences in pitch. It was found, however, that the teeth in the proximal 1/6th of the file, approximately, were rather more closely spaced than in the remainder; the density of teeth in this proximal portion is about 61–65 to the millimetre, and only 50 throughout the remainder of the file except for a few semi-isolated, more distantly-spaced teeth at the distal end. The more closely spaced teeth might produce a higher frequency of vibration in the elytra; it is suggested that this might be a mechanism producing variation in pitch, for on this basis one would expect a

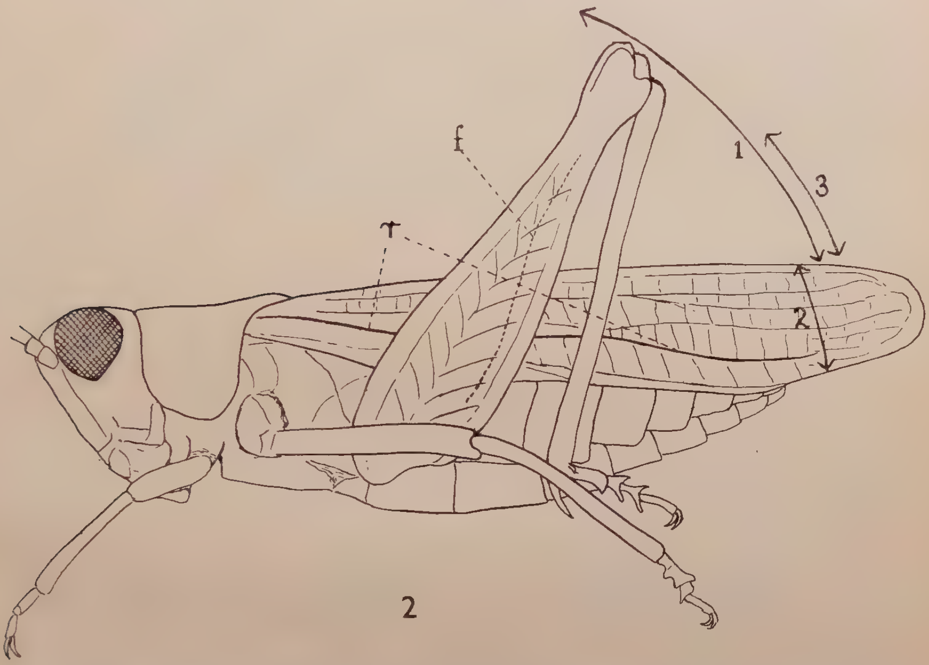


Fig. 2.—*Eremogryllus hammadae* Krauss (male). The angles 1, 2, 3 indicate the angle of vibration of the femora for the different stridulatory sounds described in the text. The dotted line (*f*) indicates the position of the stridulatory file (really on the inside of the femur); *r*, ridge on elytron. × 10.

higher note to result when the femora are elevated to a higher level. It was not established in the field, however, exactly which parts of the file and the ridge engage at different parts of the stridulation, and in any case this is clearly not the whole explanation of the differences in the sounds, which are conspicuously distinct in quality as well as in pitch ; there is room for a careful study, under laboratory conditions, of sound-production by *Eremogryllus* or other Acridids with a similar mechanism.

It is therefore clear from the foregoing account that we have in *Eremogryllus hammadae* a very complex condition as regards stridulation ; at least three patterns are found. In the present state of knowledge it is not possible to state what is the reason for such a condition ; it may be that the insects are able to produce several " songs," and employ them on different occasions according to the type of activity with which the stridulation is connected (the most probable explanation) ; or they may produce different songs under varying external conditions (this is unlikely, as the conditions at Nalut and Tripoli were roughly similar) ; or again, geographical isolation of populations may have resulted in divergent evolution in stridulation, but this is improbable as far as the Tripolitanian colonies are concerned, in view of their close proximity.

Book Notices.

A Bibliographical Supplement to " Coleoptera or Beetles East of the Great Plains," applying particularly to Western United States. By J. Gordon Edwards. 8vo. San José, Calif. (published by the Author), 1950. Pp. 183–212. Price $0.50.

This Bibliographical Supplement to the author's *Coleoptera or Beetles East of the Great Plains* is intended to provide supplementary information only for the western portions of the United States. It is in the same format as and continuously paged with the original volume.

As in the earlier volume, some of the families recognized are unfamiliar to European workers, who still regard them as of subfamily status only, a particular example being the fragmentation of the family Curculionidae into thirteen separate families.

The Principles of Insect Physiology. By V. B. Wigglesworth, M.D., F.R.S. 4th edition, revised. 8vo. London (Methuen), 1950. Pp. viii + 544, 355 figs. Price 42*s*.

The first edition has been increased by 110 pp. and 39 figs. The original arrangement is closely followed, and no completely new section has been added. On the other hand, every paragraph has been expanded and brought up to date, incorporating the work of the last ten years, and the appropriate references have been added to the list at the end of each chapter. Chapter III, " Growth," for example, now has 54 pp. and 318 references in place of 43 pp. and 205 references in 1939. Most of the original figures have been retained, though a few have been modified.

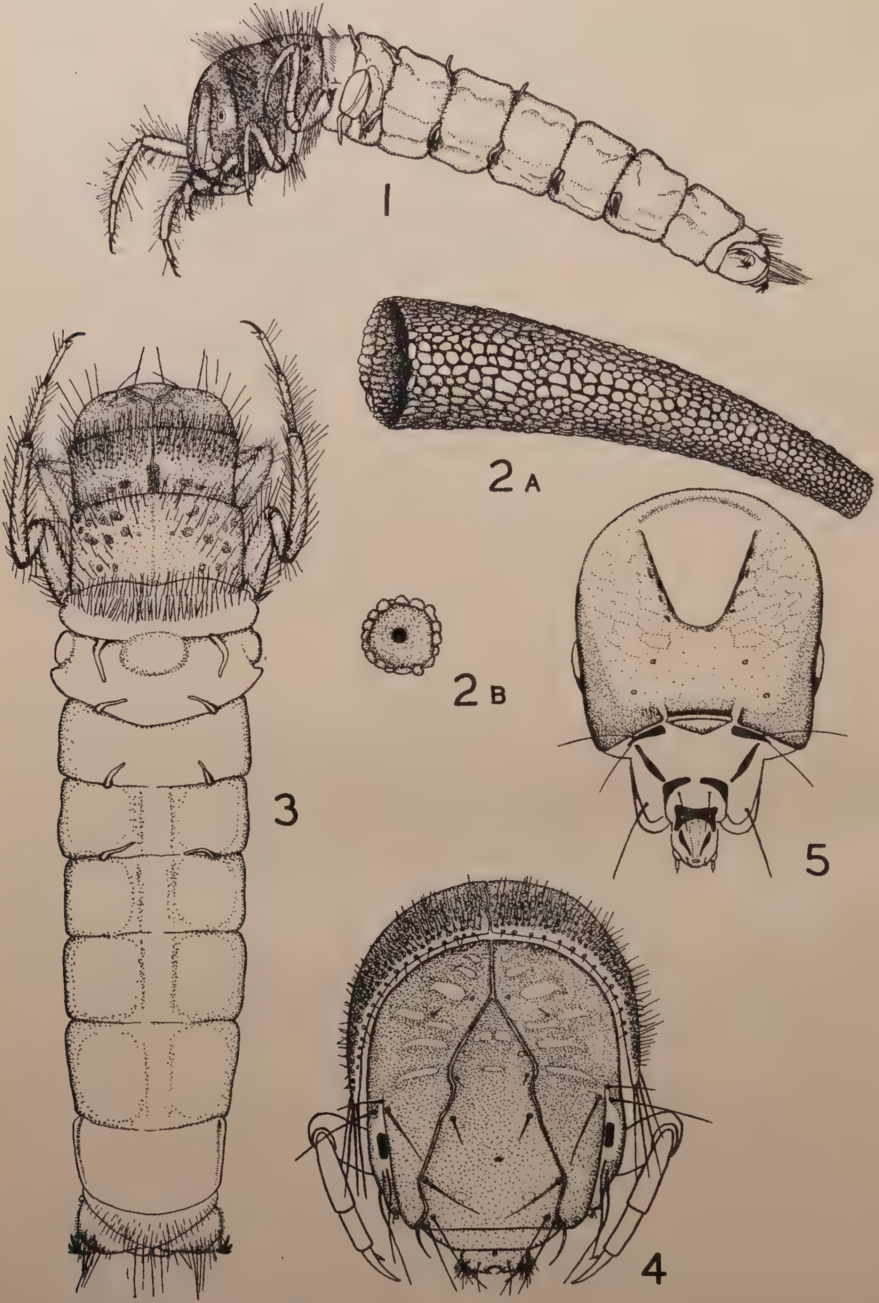
LARVAE OF THE BRITISH TRICHOPTERA.—32.

By N. E. Hickin, Ph.D., F.R.E.S.

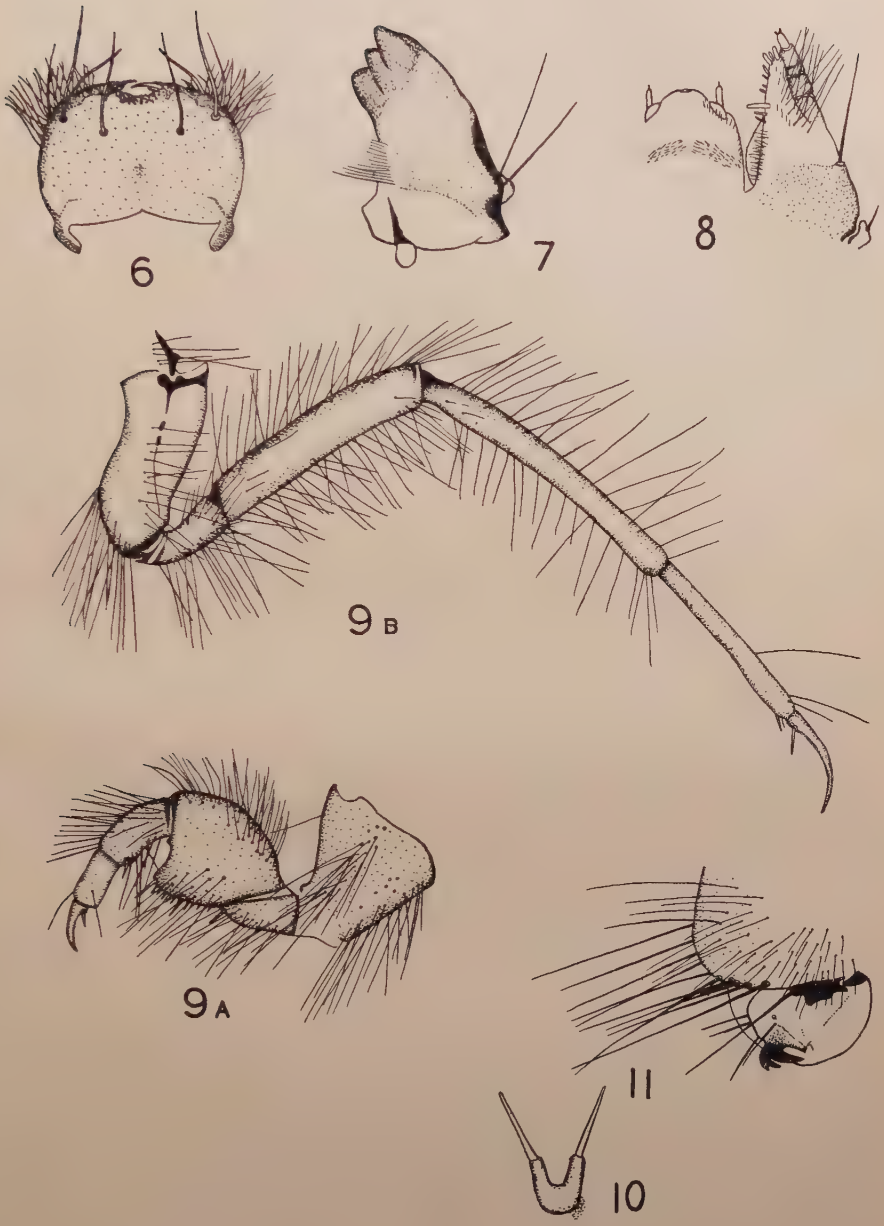
Sericostoma personatum Spence. (Sericostomatidae).

In 1936 the late Mr. Martin Mosely gave me some larvae of this species. I have checked the description and figures I made of them against larvae obtained for me by Mr. S. Nield and Mr. Thompson of the Freshwater Biological Association from Lake Windermere during 1949. *S. personatum* is fairly widely distributed, the larvae inhabiting rather fast streams, rivers and lakes where streams run into them. Two species only in the sub-family Sericostomatinae are known in the British list, the other species being *Notidobia ciliaris* Linné. I am not familiar with this latter larva, which inhabits slow-moving rivers, but the more strongly sclerotized mesonotum should be sufficient to distinguish it from *S. personatum*.

Larva: Eruciform. Head orthognathous, body strongly arched (figs. 1 and 3). Length 12 mm., width 2·5 mm. Widest at metanotum and first abdominal segment, then gradually decreasing posteriorly. *Case* (fig. 2*a*): Of sand-grains, curved and tapering posteriorly. The delicate mosaic of the sand-grains and the smooth outer surface of this case has frequently been commented upon. Posterior end sealed with secretion except for small circular opening in centre of disc (fig. 2*b*). *Head* (fig. 4): Oval when seen from the front and dark brown in colour, with a pattern of light marks on the genae and the aboral region of the clypeus; almost all the light marks are pear-shaped, with the narrow region directed away from the clypeus. Eyes prominent, situated in pale areas. Antennae small, but each bearing a small bristle. The head is considerably retracted into the prothorax and the anterior apices of the pronotum reach to a position just posterior to the eyes, and the bristles which arise from these apices appear to play a part usually played by bristles arising from the head. *Gular sclerite* not defined by sutures as is usual in the Trichoptera, only the oral region being differentiated; the aboral region is fused with the genae (fig. 5). Pattern of fine reticulated markings on ventral surface of genae. *Mandibles* (fig. 7): Four teeth. Brush of hairs on the inner edge and a pair of bristles on the base of the outer edge present on each mandible. Triangular protuberance on the outer margin near the insertion of the bristles. *Labrum* (fig. 6): The four transverse bristles long, curved and light in colour. The posterior hairs (on the lateral margins) of the bunches longer than the inner, anterior hairs. Anterior excision deep, flanked by pair of curved overlapping bristles lying in front of peg-like projections. *Thorax* (fig. 3): Pronotum heavily sclerotized and dark greyish-brown in colour. Anterior half very hairy with a few dark marks in the posterior half. Anterior margin pale and furnished with a series of pale spine-like hairs. Mesonotum much lighter in colour and not nearly so heavily sclerotized as the pronotum. Indeed some authors have described the mesonotum as membranous, and the two transverse bands of dark marks in the anterior region have been described as sclerotized patches. Metanotum membranous, with two transverse bands of black hairs. Prosternal horn absent. *Prothoracic legs* (fig. 9*a*) short, thick and very hairy (except tarsus), *metathoracic legs* long, thin and hairy (except tarsus),



FIGS. 1–5.—(1) *Sericostoma personatum*. Lateral view of larva. (2) (*a*) Larval case. (*b*) Posterior end of case from behind. (3) Dorsal view of larva. (4) Head with view of pronotum and prothoracic legs from the front. (5) Head from behind, maxillae and mandibles not drawn.



FIGS. 6–11.—(6) Labrum. (7) Right mandible. (8) Maxilla and labium. (9) (*a*) Prothoracic leg. (*b*) Metathoracic leg. (10) Sclerotized abdominal tubercle. (11) Anal claw.

meso- legs intermediate in length. *Abdomen:* Cream in colour, tapering posteriorly. Lateral line only shown by sclerotized tubercles present on 3rd to 7th segments; they are minute, however, except on the 7th segment, where a row of 14 occur on each side. They are reddish brown in colour, each with the finger-like processes (fig. 10). Sclerite on 8th abdominal segment absent but many hairs present. Protuberances on 1st abdominal segments flattened and disc-like. Gills present, either simple filiform or in small bunches. They arise from the anterior border of the segments, although Silfvenius considered that post-segmental gills also occur. An examination of the gills in the larvae in my collection shows them to be much more variable in number than Silfvenius indicates. Anal claws (fig. 11) consist of three superimposed barbs.

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BOOK NOTICES.

Gall Midges of economic importance. Vol. V. Trees. By H. F. BARNES, M.A.(Oxford), Ph.D.(London). 8vo. London (Crosby Lockwood and Son), 1951. Pp. 270, 8 pls. Price 15*s*.

Continues the series with the same format as the previous parts. The author's Preface in this, as in other volumes, forms part of a general account of the biology of gall midges, and their incidence in the Vegetable Kingdom.

Biology of Drosophila. Edited by M. DEMEREC. 8vo. New York (John Wiley); London (Chapman and Hall), 1950. Pp. x + 632, 341 figs. Price 80*s*.

Not about the biology of *Drosophila* at all, but about ontogeny and external and internal structure. The sections are: Normal spermatogenesis in *Drosophila*, by Kenneth W. Cooper; the early embryology of *D. melanogaster*, by B. P. Sonnenblick; histogenesis, organogenesis and differentiation in the embryo of *D. melanogaster*, by D. F. Poulson; postembryonic development of *Drosophila*, by Dietrich Bodenstein; external morphology of adult, by G. F. Ferris; internal anatomy and histology of image of *D. melanogaster*, by Albert Miller; collection and laboratory culture, by Warren P. Spencer.

The book is an exhaustive account of what are considered to be the natural structure and development of *D. melanogaster*, a standard against which experimental modifications can be assessed.

APHID EXCRETION.

By L. Broadbent, Ph.D., F.R.E.S.
(*Rothamsted Experimental Station, Harpenden, Herts.*)

The sweet sticky excretion of aphids commonly called " honeydew " has been widely known for centuries, but there are few references in the literature to the methods whereby it is excreted. Kirby and Spence (1843) stated : " When no ants attend them, by a certain jerk of the body, which takes place at regular intervals, they ejaculate it to a distance." Buckton (1876) reported : " the forcible ejection of a liquid from (the anus) . . . of the full-fed individuals of a colony of *Lachnus saligna* (= *Tuberolachnus saligna* (Gmelin)), . . . which infests the willow tree. . . . Many of these insects will . . . erect the terminal rings of their bodies, upon the apex of which a clear drop of fluid will, for a moment, appear. If this is not quickly withdrawn by an attendant ant . . . it is projected by a peculiar jerk to a considerable distance." Weber (1930) stated that in Homoptera very diverse structures have been developed which facilitate excretion and which, above all, allow the stream of excrement to take a safe direction. In aphids the anus forms a valve, which is directed backwardly above, and the dorsal region of which is generally drawn out to a tail or cauda. He said that the cauda is raised by special muscles, the anus opened, and the excrement driven out by the musculature of the rectum.

Smith (1937) used the rate of deposition of honeydew by *Hyalopterus pruni* (Geoff.) as a measure of the rate of feeding, and incidentally described the method of excretion in these words : " The tip of the abdomen is raised, a globule of transparent colourless liquid is secreted and held for an instant on the tip of the abdomen. The left posterior leg is then swung upward and outward. The drop of excrement is caught by the tip of the tibia and base of the tarsus and thrown with considerable force. From a height of 6 in. females frequently throw excrement laterally for a distance of 6 to 8 in. The mass of each droplet and force and direction of the throw are remarkably uniform."

My observations suggest that Smith must have watched only the nymphs, for which the above description is almost adequate. The following observations may be added : Aphids excreted only while feeding, and balanced themselves each on their proboscis and anterior two pairs of legs when the abdomen was raised. After raising the abdomen until it was almost at right angles to the leaf, the posterior pair of legs of the nymph was waved in the air for a few seconds ; then a few tentative kicks were made with the leg which was to despatch the globule. Finally the aphid remained rigid for a moment, the globule appeared suddenly and was held on the anus for one or two seconds, then was kicked off as described by Smith. Either leg was used to kick the globule, whose diameter was about the width of the aphid's head.

The adult aphids, both alatae and apterae, raised their abdomen in the air, cauda and cornicles rose till they were almost at right angles to the body (at least, in species with long cornicles), and though they occasionally waved their posterior legs a few times before the globule appeared, they kept them still while the globule remained poised on the anus for one or two seconds before being flicked off by the cauda, which was first flexed back dorsally and then suddenly returned to its normal position, striking the globule as it did so. Many aphids raised the abdomen some way without removing their legs from the plant.

This process was essentially the same in all the "free-living" forms studied, with the exception of *Brevicoryne brassicae* (L.). By "free-living" are meant aphids which live on the stems or leaves of plants without forming galls or pseudogalls; root-feeders are not included. The species studied were:

Macrosiphum euphorbiae (Thomas) on *Tulipa* sp.
Macrosiphum rosae (L.) on *Rosa* sp.
Macrosiphoniella millefolii (De Geer) on *Achillea millefolium.*
Acyrthosiphon pisum (Harris) on *Lathyrus* sp.
Dactynotus (*Uromelan*) *jaceae* (L.) on *Centaurea nigra.*
Myzus cerasi (Fabr.) on *Prunus cerasus.*
Myzus persicae (Sulzer) on *Brassica rapa.*
Aulacorthum solani (Kalt.) on *Solanum tuberosum.*
Hyalopterus pruni (Geoff.) on *Prunus amygdalus.*
Rhopalosiphum nymphaeae (L.) on *Nymphaea alba.*
Aphis fabae Scop. (?) on *Tropaeolum* sp.
Aphis grossulariae (Kalt.) on *Ribes grossularia.*
Brachycaudus cardui (L.) on *Chrysanthemum leucanthemum.*
Periphyllus testudinatus (Thornton) on *Acer pseudo-platanus.*

In *A. fabae* the globules were larger than in the other species, and their discharge left the end of the abdomen considerably deflated. The discharge of the globules by the adults in *H. pruni* and *P. testudinatus* was more rapid than in the other species.

All instars of apterous *Brevicoryne brassicae* on *Brassica campestris* raised their abdomens and often waved their posterior legs in the air and scraped them back and forth over the abdomen before the globules appeared. But just before the emergence of the globule the aphid became rigid and remained so for a number of minutes with the globule poised on its anus. The longest time recorded for this posture (in 20 aphids) was 19·0 minutes by an adult, the shortest being 6·2 minutes by a 2nd instar nymph. The average for the 20 aphids (second, third, fourth and fifth instars) was 11·0 minutes. During this time the fluid evaporated and became more viscous (this was tested with a needle), and the globule shrank to about half of its original diameter. It was then rubbed with the tibiae of the posterior legs, being twisted about on the anus as a pivot, and coated with wax from the legs. It was soon disengaged from the anus, and being scraped off one leg with the other, fell on to the nearest piece of plant, aphid or ground. If a particle of wax got on to the surface of the globule when it was poised on the anus, it was in constant motion.

Only one of fifteen apterous adults studied departed from this procedure; with this aphid a small globule emerged twice during a period of ten minutes and was reabsorbed. There was the usual leg-waving at intervals during this time; then the legs were still and a large globule appeared, which after a moment was ejected, presumably by the cauda. This globule hit a leaf hair and evaporated in about 15 minutes. Alate *B. brassicae*, on the other hand, excreted like other "free-living" aphids.

A number of gall-forming or leaf-rolling aphids have been studied; all were covered with wax to a degree which varied from species to species, and excretory mechanisms also varied.

Hayhurstia atriplicis (L.) in leaf pseudogalls on *Chenopodium vulvaria* excreted in the manner of most "free-living" aphids, but the globules soon became coated with wax from contact with the mealy wax covering of the aphids and the loose wax particles on the leaf. Globules often coalesced to form one or more large wax-covered globules in the gall. Mr. V. Eastop reported similar globules in galls of *Semiaphis cucubali* (Pass.) on *Silene* sp., but these aphids were not seen to excrete.

Holcaphis frequens (Walker) on *Agropyrum repens* feeds within the longitudinally curled leaves. Some of the light mealy covering of the aphids becomes deposited on the leaf surface. Nymphs of this species tried to kick off the globules of honeydew, but their short legs would not reach and the tarsus only touched the globule, which stuck to it and was lowered to the leaf. Adults projected the globules with their cauda. The globules soon became coated with wax from the aphids' bodies and leaf surface.

Eriosoma ulmi (L.) in rolled leaves on *Ulmus campestris* was covered with flocculent wax. No attempt was made to dislodge the globule of honeydew when it emerged, and it remained on the anus until it was rubbed off by contact with other aphids or the leaf. It always quickly became covered with wax. Similar globules of wax-covered honeydew were found in galls of *Eriosoma lanuginosum* (Hartig) on *Ulmus campestris* (reported by Mr. Eastop).

Eriosoma lanigerum (Hausmann) on *Pyrus malus* was so densely covered with wax that the drops of honeydew remained caught in the wax around the aphid until evaporation caused the globule to become first very viscous and then solid.

Byrsocrypta bursaria (L.) in galls on *Populus nigra* were covered with wax, particularly at the posterior end. As in *Eriosoma* spp., no attempt was made to dislodge the globule of honeydew, which stayed on the anus until movement by that or another aphid caused it to be knocked off. The globule gathered wax as it passed through the mass of wax around the anus.

In the gall-living aphids examined the insects moved among the mass of wax-coated globules without much inconvenience and without getting stuck. The globules remained fluid for a considerable time, the wax coating and high humidity within the gall preventing rapid evaporation.

Two species of soil-inhabiting aphids have been examined. *Anuraphis subterranea* (Walker) was feeding at the base of the stem of *Heracleum sphondylium* just below soil level. Of five nymphs studied, four reared their abdomen and kicked their legs, but did not violently kick off the globule when it appeared. They caught it gently on one leg and lowered it to the soil, where it immediately soaked in. In the fifth nymph the globule remained on the anus for 15 minutes, but did not evaporate and become viscous as with *B. brassicae*, and it soaked in as soon as it touched the soil when the aphid moved. In the adult apterous stage the globule appeared to drop from the anus, but was presumably gently knocked off by the cauda, and soaked in.

In an apparently undescribed species of *Protrama* feeding on the roots of *Sonchus arvensis* the globule appeared and stayed on the anus until it touched the soil, when it immediately soaked in. The aphids made no attempt to kick the globules, though they waved their very mobile posterior legs over their backs and heads as described by Donisthorpe (1927).

MEASUREMENT OF THE RATE OF EXCRETION.

Smith (1937) used the rate of deposition of honeydew to measure the rate of feeding of *H. pruni*. The drops of honeydew were caught on sheets of paper coated with bromo-cresol green and mounted on revolving clocks below the feeding aphids. He found that the rate of excretion increased with increasing temperature, but that this rate did not increase as rapidly as the rate of reproduction. He concluded that this indicated relative starvation at higher temperatures, which was a primary cause of wing determination. Schaefer (1938) found more honeydew was produced by uncrowded than by crowded aphids. None was produced by fasting aphids. He demonstrated rapid evaporation of moisture from the body of the insect, and pointed out that Smith's results might be due to evaporation and not to lack of intake of food. He concluded that lack of fluid, together with rapid evaporation from the body of the parent, caused a concentration of waste substances which appeared to initiate wing development.

The effect of evaporation on rate of excretion was studied in a wind tunnel, using *M. persicae* feeding on cabbage, with the bromo-cresol green indicator papers mounted on 24-hour clocks. Two experiments were made with single aphids; the tunnel was lit with fluorescent lamps throughout the experiment, and a 2 m.p.h. wind was alternated with still air over periods of 24 hours. The rate of excretion was less in the wind in both experiments (Table I), indicating that either the aphid fed less or, more likely, that the rate of evaporation of moisture from the general body surface was greater. This confirms Schaefer's view that rate of deposition of honeydew cannot be used to measure rate of feeding reliably when external conditions vary.

TABLE I.—*Mean Intervals (mins.) between Drops of Excreta of* M. persicae *Feeding on Cabbage over 24-hour Periods in Still Air and in a 2 m.p.h. Wind.*

	Wind.	Still air.	Temperature. (° C.).
Exp. 1 (1 day each)	37	28	17·5–21·0
Exp. 2 (2 days each)	35	25	17·5–21·0

By means of bromo-cresol green indicator paper it was confirmed also that *M. persicae* does not excrete unless it is feeding, and that feeding and excretion take place continuously in light or darkness. Smith found that *H. pruni* often ceased excreting for a few hours after periods of excretion of from 2 to 15 hours. Although the rate of excretion of *M. persicae* varied somewhat, possibly as a result of temperature differences, it did not cease for long periods except when an aphid cast its skin or moved its position. The aphid in Exp. 2 did not move its position during the four days of the experiment. A fourth instar nymph ceased excreting for 2 hr. 50 min. during ecdysis; on another occasion a second instar ceased for 7 hr. 40 min. Adults did not stop excreting while producing young.

DISCUSSION.

A few species only have yet been examined, but the diversity of excretory habits shown by these species suggests that the subject merits further study. The differences may be the result of modifications due to habitat, but they may also help to elucidate the phylogeny of the APHIDIDAE.

Is the development of a copious wax covering a necessary adjunct to life in confined quarters such as a gall ? In the absence of wax the aphids presumably would soon become covered with their own sticky honeydew and the gall would be uninhabitable. All gall-living aphids and many of those living in curled leaves are wax-covered. Presumably aphids would not like conditions inside a confined space if they were frequently projecting their honeydew with considerable force, and although *H. atriplicis* behaved thus in the leaf-pseudo-galls of *Chenopodium*, the other gall-forming aphids examined did not forcibly dislodge the globules, but allowed them to be knocked off. Theobald (1929), describing *E. ulmi*, stated : " under this curled leaf we find the apterae amongst a lot of meal, flocculent matter and mealy-coated oil globules of a saccharine nature." These are the wax-covered globules of honeydew described above. Theobald described wax-covered aphids and globules also in *Tetraneura ulmifoliae* Baker (= *gallarum* (Gmelin)) in galls on *Ulmus* spp. ; in *Eriosoma lanigerum* in curled leaves of *Ulmus* spp., and in *Hyalopterus melanocephalus* (Buckt.) (= *Semiaphis cucubali*—see above). Buckton (1876) recognized the nature of the globules : " These globules are faecal matter, discharged from the anus of the insects, which swarm within the curled leaves, and their spherical form is due to the presence of the fine meal-like powder taken from the bodies of the Aphides. . . . By this peculiar dusting of their surfaces the insects are not incommoded by their own excreta. . . . It is possible that the hoariness of some species may be a protection to them from rain very much in the same manner." He described similar wax-covered globules also in " *Cryptosiphum silenes* (= *Cryptosiphum gallarum* (Kalt.)), and likewise in other close habitations of aphides."

Although most wax-covered aphids live in confined spaces, several apparently free-living species are covered with meal or wax. Such are *Phloeomyzus passerinii* (Sign.) on *Populus alba*, *Lachnus costatus* (Zett.) on *Pinus* spp., etc., *Schizolachnus tomentosus* (De Geer) on *Pinus* spp., *Asiphum tremulae* (De Geer) on *Populus tremulae*, *Phyllaphis fagi* (L.) on *Fagus sylvatica*, and *Brevicoryne brassicae* on many brassica hosts. Of *P. fagi* Theobald wrote : " By means of this wool they form a dense white mass beneath the leaves. Buckton says that occasionally this excrement accumulates into resinous lumps which Walker refers to as being sweet." This sounds similar to the condition found in *E. lanigerum*, described above. The excretory mechanisms in these aphids need to be studied before speculations can be made about their phylogeny, but apterous *B. brassicae* are not only densely covered with wax, but do not forcibly project the globules of honeydew. The question naturally arises, therefore, as to whether or not *B. brassicae* has developed from a gall-living species. Many gall-living and leaf-curling species migrate to other hosts during the summer, and although they frequently live on the roots of these secondary hosts, it may be that the ancestor of *B. brassicae* once behaved in this manner, but that later it took to spending its whole life cycle on brassica hosts, some one or other of which remain alive throughout the year.

The honeydew of the two soil-inhabiting aphids studied soaked into the soil very rapidly. In such forms there is little need for the projection of honeydew to clear the colony, or of wax to confine the globules, although some soil-inhabiting aphids produce much wax, e.g., *Pachypappella piceae* (Hartig) and *Byrsocrypta bursaria*. Further, many soil aphids are tended by ants for their honeydew, and these will act as scavengers. Darwin (1859) was of the opinion that aphids excreted purposely in response to the ants' movements. He wrote : " I removed all the ants from a group of about a dozen aphides on a dock-plant, and prevented their attendance during several hours. After this interval I felt sure that the aphides would want to excrete. I watched them for some time through a lens, but not one excreted ; I then tickled and stroked them with a hair in the same manner, as well as I could, as the ants do with their antennae ; but not one excreted. Afterwards I allowed an ant to visit them, . . . it then began to play with its antennae on the abdomen first of one aphis and then of another ; and each, as soon as it felt the antennae, immediately lifted up its abdomen and excreted a limpid drop of sweet juice, which was eagerly devoured by the ant . . . if the (ants) be not present they are at last compelled to eject their excretion. But as the excretion is extremely viscid, it is no doubt a convenience to the aphides to have it removed ; therefore probably they do not excrete solely for the good of the ants." *A. grossulariae* on *Ribes grossularia* did not respond to the ants which tended them, but excreted in the usual manner of ' free-living ' aphids. The ants quickly discovered and devoured any globule which landed on the colony or on a nearby leaf. Kirby and Spence (1843) stated that ants both take advantage of any excretion and also solicit it.

Is the cauda in aphids an appendage which has developed to aid excretion ? Theobald (1926) wrote : " The cauda varies much in size in the various genera ; it may be very small as in *Pemphigus* (i.e., *Byrsocrypta*) and *Eriosoma* and *Geoica* or very long as in *Macrosiphum*. In shape it may be ensiform, clavate or triangular, rounded or acuminate. . . . It only assumes its typical form in the fully matured apterae and alatae ; in the immature form it is always smaller and usually bluntly triangulate." It will be noted that the genera which Theobald selected to illustrate very small cauda are either gall-making forms or are myrmecophilous, genera which do not need to, nor do they, project their honeydew to a distance. All adults of the " free-living " forms examined had caudae adequate for aiding excretion, whereas nymphs never had well-developed caudae and had to use their legs to kick off the honeydew globules. Apterous *B. brassicae* had apparently adequate caudae, but they rarely used them to project honeydew. Alatae had larger and more effective caudae.

Mr. V. Eastop kindly collected *M. millifolii*, *D. jaceae*, *H. atriplicis*, *H. frequens*, *E. lanigerum* and *A. subterranea*.

SUMMARY.

The excretory habits of 22 species of aphids were studied. Most species living freely on leaves or stems raised their abdomen and stayed still while a globule of honeydew appeared ; the globule was poised on the anus for one or two seconds until flicked off by the cauda. Nymphs kicked off the globule with a back leg. Modifications of these methods by aphids living in galls and underground are described. Aphids did not excrete except when feeding; feeding and excretion continued in darkness. Nymphs did not excrete during ecdysis, but adults continued at their usual rate when producing young. Evaporation affected the rate of excretion. It is suggested that wax and caudal development might be related to excretory habits.

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BOOK NOTICE.

Verzeichnis der Kaefer Mitteleuropas (*Deutschland, Österreich, Tschechoslovakei*) *mit kurzen faunistischen Angaben.* Von AD. HORION. Abt. 1, Caraboidea, Palpicornia, Staphylinoidea, Malacodermata, Sternoxia, Fossipedes, Macrodactylia, Brachymera. 8vo. Stuttgart (Alfred Kernen Verlag), 1951. Pp. x + 266. Price 12 DM.

This Catalogue of the Beetles of Central Europe is an attempt to bring up-to-date the Schilsky Catalogue, *Mitteleuropaische Kaeferverzeichnis*, 1909. The systematic arrangement followed is that adopted in Winkler's *Catalogus Coleopterorum regionis Palaearcticae* (1924–1932) except where later work has rendered that out-of-date.

The Catalogue is difficult to use, at first sight, owing to an excessive abbreviation of the entries; the key page of the abbreviations used is unattached, presumably to facilitate use, but it could be easily mislaid and, if it were lost, the usefulness of the volume would be seriously diminished! Perhaps a more continuous acquaintance with the volume would enable the memorizing of the abbreviations.

The volume is published in typescript owing to the high cost of printing.

ON THE URTICATING PROPERTIES OF ADULT LYMANTRIIDAE.

By A. N. Clements.

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Eltringham (1913) described how the larva of *Euproctis similis* Fuess. sheds its urticating spicules in a band on the inside of the cocoon. These are picked up by the female moth in its anal tuft on emergence from the pupa. The female anal tuft contains barbed hairs to pick up and hold the spicules, and these with the spicules are later shed as a covering over the eggs. Gilmer (1925) suggests that the urticating properties of adults of related genera owe their origin to a similar habit. There are many accounts of urtication following contact with adult Lymantriidae, mostly *Euproctis*, from many parts of the world, in particular from China and Japan. Matheson (1950) and Illingworth (1926) give a number of references. It seemed likely that examination of the anal tufts of female Lymantriidae for larval spicules would show the extent of this habit in the Lymantriidae, and the present study was therefore undertaken on the Lymantriidae in the British Museum (Natural History) and on moths of other families with known urticating properties. At least two species of each genus were examined if females were available.

Of the fifty species of *Euproctis* examined all but two were found to hold larval spicules in the anal tuft. Neither of these two species, *E. melanoma* Collnt. and *E. pauperata* Leech, bore the typical adult barbed hairs, and further, in a long series of *E. pauperata* the anal tuft appeared to be entirely absent. It is, of course, possible that both larval spicules and adult barbed hairs had previously been shed in all the specimens examined. Only observation of the life history can prove the absence of the habit in these two species, but its absence appears likely. Also it is possible that these species are wrongly placed in *Euproctis*. Among the species of *Euproctis* where the female moth picks up the larval spicules considerable differences were found in the extent of the barbing of the adult hairs. Most frequently the hairs were barbed for about one-third of their length (fig. 1, c). In a few species the barbs were confined to the tip (fig. 1, b), while in *E. xuthocloea* Collnt. (fig. 1, a) the barbs were entirely absent.

Larval spicules were also found in the anal tufts of the following Lymantriid genera: *Acyphas*, *Albarracina*, *Cozola*, *Medama*, *Parakanchia* and *Porthmeia*. In each case the hairs on the anal tuft were also barbed. In the genera *Jacksonia*, *Lacida*, *Lacipa*, *Laelia*, *Marblepsis* and *Olapa* the anal tuft of some species contained barbed hairs but no larval spicules.

No larval spicules were found in the anal tuft in families other than the Lymantriidae. However, in *Ochrogaster* and *Gazalina* (Notodontidae) the hairs of the female anal tuft were minutely barbed, and in *Gazalina chrysolopha* Koller spicules were found on the larva very similar to those of *Euproctis* (fig. 1, j and k), but no spicules were found in the anal tufts of the females examined. In all other genera examined, including *Anaphe*, the hairs of the anal tuft were smooth.

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As is well known, the LYMANTRIIDAE often have a tuft of hair at the tip of the abdomen which is used to cover the eggs. The habit is described by Comstock (1920) in *Lymantria dispar* L., by Wileman (1918) in *L. mathura* Moore, and by South (1920) in *Dasychira fascelina* L. These three species were examined for larval spicules but none was found in the anal tufts. It appears that the habit of shedding the anal tuft over the eggs is widespread in the LYMANTRIIDAE, and in some species the hairs have developed barbs to provide for a more compact mat over the eggs, not necessarily to hold the larval spicules. Knight (1922) states that the flimsy cocoons of *Hemerocampa leucostigma* Sm. and Abb. are interwoven with the hairs from the body of the caterpillar, and showed the cocoons to have marked urticating properties. No urticating spicules were found in the anal tufts of this species, so the spicules must be interwoven in the cocoon for the protection of the pupa alone.

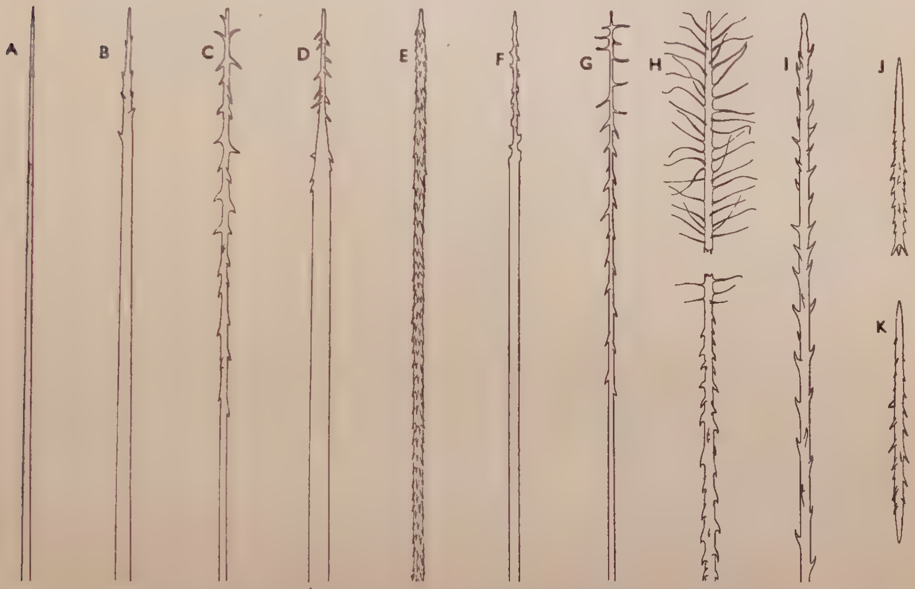

FIG. 1.—A–I, hairs of female anal tuft. A, *Euproctis xuthocloea* Collnt. B, *E. virgo* Swin. C, *E. aroa* B.-Bkr. D, *E. epichrysa* Collnt. E, *Gazalina chrysolopha* Koller (Notodontidae). F, *Parakanchia grisea* B.-Bkr. G, *Cozola leucospila* Walk. H, *Jacksonia striata* Collnt. I, *Olapa macrocerca* Collnt. J–K, larval spicules. J, *Euproctis paradoxa* Butl. K, *Gazalina chrysolopha* Koller (Notodontidae).

In the LYMANTRIIDAE two distinct habits have evolved, that of shedding the larval hairs in the cocoon to protect the pupa, and that of shedding the hairs of the anal tuft over the egg mass to protect the eggs. In *Acyphas*, *Albarracina*, *Cozola*, *Euproctis*, *Parakanchia*, *Porthmeia* and *Medama* the two habits are combined, and the larval spicules shed in the cocoon for the protection of the pupa are collected by the female and shed with its own hairs over the eggs.

TABLE I.—*Results of an Examination of the Anal Tufts of* LYMANTRIIDAE.

1. Species of *Euproctis* in which the anal tuft was composed of barbed hairs and contained larval spicules :

alba Swinhoe, *aliena* Butler, *argentimarginata* Wileman, *aroa* Bethune-Baker, *biagi* Bethune-Baker, *bigutta* Walker, *camellia* Collenette, *chrysorrhoea* Linnaeus, *chrysosoma* Collenette, *conisalea* Collenette, *conistica* Collenette, *divisa* Walker, *enochra* Collenette, *epichrysa* Collenette, *fasciata* Walker, *frigidior* Collenette, *fusipennis* Walker, *galactopis* Turner, *glaphyra* Collenette, *hoenei* Collenette, *karapina* Strand, *latifascia* Walker, *lavella* Bethune-Baker, *lunata* Walker, *luteomarginata* Bethune-Baker, *melanosoma* Butler, *neavei* Tams, *ochacantha* Collenette, *pallens* Bethune-Baker, *paradoxa* Butler, *phaula* Collenette, *polytoca* Collenette, *pygmaea* Walker, *schaliphora* Collenette, *semivitta* Moore, *sericea* Wileman, *similis* Fuessli, *stramenta* Bethune-Baker, *stellata* Distant, *taiwana* Shiraki, *tanystola* Collenette, *thysanocyma* Collenette, *varians* Walker, *virgo* Swinhoe, *virguncula* Walker, *xanthorrhoea* Koller, *xuthocloea* Collenette (adult hairs smooth), *xuthonepha* Collenette.

2. Species of *Euproctis* in which the anal tuft was composed of smooth hairs and did not contain larval spicules :

melanoma Collenette, *pauperata* Leech.

3. Species of other genera in which the anal tuft was composed of barbed hairs and contained larval spicules :

Acyphas chionitis Turner, *A. leptotypa* Turner, *A. leucomelas* Walker, *Albarracina baui* Staudinger, *A. korbi* Staudinger, *Cozola ateralbus* Rothschild, *C. collenettei* Nieuwenhuis, *C. defecta* Strand, *C. dolichoptera* Collenette, *C. leucospila* Walker, *C. proxantha* Pagenstecher, *C. submarginata* Walker, *Medama diplaga* Hampson, *Parakanchia grisea* Bethune-Baker, *Porthmeia pyrozona* Collenette, *P. subnigra* Bethune-Baker.

4. Genera in which the anal tuft was composed of smooth hairs and did not contain larval spicules (occasional species with anal tuft composed of barbed hairs marked *) :

Abynotha preussi Mabille, *Aclonophlebia lugardi* Swinhoe, *A. rhodalipha* Felder, *Anexotamos flavibasis* Hering, *Arctornis comma* Hutton, *A. moorei* Leech, *Argyrostagma niobe* Weymer, *Aroa clara* Swinhoe, *A. subnotata* Walker, *Aruta puncticilia* Moore, *Barlowia charax* Druce, *B. zelotes* Talbot, *Barobata trocta* Korschefsky, *Birnara bicolor* Walker, *Cadurca moco* Collenette, *C. venata* Swinhoe, *Caragolina costalis* Moore, *Carriola ecnomoda* Swinhoe, *C. fenestrata* Hampson, *Casama vilis* Walker, *Cassidia obtusa* Walker, *Caviria odriana* Schaus, *C. vestalis* Schaus, *Chrysocyma fulvicolor* Hampson, *Cimola opalina* Walker, *Cispia alba* Moore, *C. charma* Swinhoe, *Cobanilla lerwa* Swinhoe, *C. marginata* Moore, *Conigephyra discolepia* Hampson, *Creagra liturata* Guerin, *Crinola flavicollis* Leech, *Cropera nigripes* Hampson, *C. testacea* Walker, *Crorema mentiens* Walker, *C. nigropunctata* Collenette, *Croremopsis argenna* Mabille, *Cymaroa leptopepla* Hampson, *Daplasa irrorata* Moore, *Dasycampa flammeola* Distant, *D. libyra* Druce, *Dasychira bacchans* Karsch, *D. fascelina* Linnaeus, *Dasychiroides bicolora* Bethune-Baker, *D. pratti* Bethune-Baker, *Dendrophleps* *semihyalina* Hampson, *Desmoloma signata* Dyar, *Dura nepha* Joicey and Talbot, *D. niveus* Bethune-Baker, *Eala hemiluta* Collenette, *Ectobema antra* Swinhoe, *E. forbesi* Druce, *Eloria copharpe* Collenette, *E. moeonia* Druce, *Eopirga candida* Hering, *E. heptasticta* Mabille, *Etobema antra* Swinhoe, *E. forbesi* Druce, *Euproctidion rhodobaphes* Collenette, *E. stricta* Collenette, *Euproctoides acrisia* Plötz, *E. ertli* Wichgraf, *Gynaephora selenitica* Esper, *Hemerocampa leucostigma* Abbot and Smith, *H. plagiata* Walker, *Heracula discivitta* Moore, *Heteronygmia flavescens* Holland, *H. manicata* Aurivillius, *Himala argentea* Walker, *Imaus munda* Walker, *Ivela auripes* Butler, *Jacksonia striata* Collenette,* *Kanchia lepta* Collenette, *Lachana ladakensis* Moore, *Lacida antica* Walker,* *L. costalis* Walker,* *Lacipa flavitincta* Hampson, *L. pseudolacipa* Hering,* *L. quadripunctata* Dewitz,* *Laelia caenosa* Hübner, *L. exclamationis* Koller,* *Laeliophila seydeli* Hering, *Laelioproctis leucosphena* Collenette, *L. taenisoma* Hering, *Leptepilepta diaphanella* Mabille, *Leptocneria binotata* Butler, *L. reducta* Walker, *Leucoma cryptadia* Collenette, *L. salicis* Linnaeus, *Locharna strigipennis* Moore, *Lomadonta eurythrina* Holland, *L. obscura* Swinhoe, *Lymantria dispar* Linnaeus, *L. mathura* Moore, *Lymantriades obliqualinea* Bethune-Baker, *Mahoba plagidotata* Walker, *Marblepsis crocipes* Boisduval, *M. macrocera* Sharpe,* *M. melanocraspis* Hampson, *Mardara calligramma* Walker, *Malachitis preangerensis* Heylaerts, *Mylantria xanthospila* Plötz, *Naroma signifera* Walker, *Neomardara africana* Holland, *Neorgyia ochracea* Bethune-Baker, *Numenes quadriplagiata* Walker, *N. siletti* Walker, *Ocneria rubea* Fabricius, *Ocnerogyia amanda* Staudinger, *Ogoa fuscovenata* Wichgraf, *O. neavei* Rothschild, *Olapa brachycerca* Collenette,* *O. crocicollis* H.-Sch., *O. macrocerca* Collenette,* *O. tavetensis* Holland, *Orgyia antiqua* Linnaeus, *O. aurolimbata* Guenée, *Otroeda hesperia* Cramer, *O. nerina* Drury, *Palasea albimacula* Wallengren, *P. gondona* Swinhoe, *Pantana delineata* Walker, *P. visum* Hübner, *Paramarbla catharia* Collenette, *P. teroensis* Collenette, *Parapirga oloris* Hering, *Paraproctis calamolopha* Collenette, *Parocneria audeoudi* Brandt, *P. detrita* Esper, *Pendria rinaria* Moore, *Penthophera morio* Linnaeus, *Perina nuda* Fabricius, *Perinetia leucocloea* Collenette, *Pernambis groenlandica* Wocke, *P. rossi* Curtis, *Pida decolorata* Walker, *P. postalba* Wileman, *Pirgula stictogonia* Collenette, *Pirga luteola* Hering, *P. magna* Swinhoe, *Polymona rufifemur* Walker, *Psalis pennatula* Fabricius, *Pseudarctia nivea* Bethune-Baker, *Pseudobazisa desperata* Hering, *P. thermochrous* Hering, *Pteredoa crystalloides* Collenette, *P. plumosa* Hampson, *Redoa egens* Felder, *R. submarginata* Walker, *Rhypopteryx sordida* Aurivillius, *Rolepa erica* Schaus, *Ruanda aetheria* Strand, *Sarsina dirphioides* Walker, *S. festiva* Schaus, *Scaphocera marginepunctata* Saalmüller, *Scarpona ennomoides* Walker, *Sitvia denudata* Walker, *S. karoli* Semper, *Somatoxena lasea* Druce, *Sorocaba anomala* Moore, *Sphragista kitchingi* Bethune-Baker, *Stracilla ghesquerei* Collenette, *S. translucida* Oberthür, *Staetherinia corydona* Druce, *S. semilutea* Walker, *Stracena fascivena* Swinhoe, *S. promelaena* Holland, *Stilpnaroma venosa* Hering, *Synogdoa simplex* Aurivillius, *Tearosoma aspersum* Felder, *Thagona parmata* Druce, *T. unicolor* Schaus, *Topomesoides jonasii* Butler, *Varmina indica* Walker.

SUMMARY.

Two distinct habits have evolved in the LYMANTRIIDAE, one of shedding the larval hairs in the cocoon to protect the pupa and another of shedding the hairs of the anal tuft over the egg mass to protect the eggs. In *Acyphas*, *Albarracina*, *Cozola*, *Euproctis*, *Parakanchia*, *Porthmeia* and *Medama* the two habits are combined, and the larval spicules shed in the cocoon for the protection of the pupa are collected by the female and shed with its own hairs over the eggs.

ACKNOWLEDGMENTS.

I am grateful to Dr. H. E. Hinton for bringing this problem to my notice. To Mr. C. L. Collenette I am glad to express my warmest thanks for the benefit of his wide knowledge of the LYMANTRIIDAE, and the help which he readily gave made the work much easier. The work was made possible by a grant from the Trustees of the British Museum (Natural History), for which I am grateful.

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BOOK NOTICE.

Chemical Control of Insects. By T. F. WEST, J. ELIOT HARDY and J. H. FORD. 8vo. London (Chapman and Hall), 1951. Pp. xi + 211, 44 figs. Price 15*s*.

A summary of insecticides, chemical attractants and repellants, and selective weed-killers. Introductory chapters review the insect in relation to its physical environment and the principles of insect control. The insecticides are classified into fumigants ; nicotine compounds ; rotenone and allied compounds ; arsenicals ; petroleum oils ; coal-tar derivatives ; " miscellaneous," including sulphur compounds and fluorides ; soil insecticides, such as carbon disulphide and chloropicrin ; chlorinated persistent insecticides, i.e., DDT and BHC. Repellants and attractants are dealt with in a separate chapter, and there is an account for 2·4-D and other selective weed-killers. Molecular structure is given for the principal compounds, and there is a bibliography to each chapter.

EXPERIMENTAL HYBRIDIZATION OF *ANOPHELES MACULIPENNIS* VAR. *ATROPARVUS* MEIGEN AND *ANOPHELES QUADRIMACULATUS* SAY.

By M. Maryon, P. Lee and P. G. Shute.

(*Medical Research Council Malaria Reference Laboratory, Horton Hospital, Epsom.*)

This experiment was instituted to ascertain whether there was any possibility of hybridization between *Anopheles maculipennis* var. *atroparvus* and *Anopheles quadrimaculatus*.

Both *atroparvus* and *quadrimaculatus* are efficient malaria carriers. The former is an important carrier in western and southern parts of Europe, and the latter is the most important carrier in the south-eastern United States.

The mosquitoes used in this experiment were bred in the laboratory. The *atroparvus* were first obtained from the Isle of Grain, Kent, in 1933, and have been bred continuously in the laboratory since that date. The *quadrimaculatus* were obtained in 1946 through the kindness of Dr. Hawking of the Institute for Medical Research. The strain was brought back by him from the United States of America.

Method.

Each species of mosquito up to the pupa stage was kept in a separate insectarium with a temperature of 75°–80° F. Each pupa of each species was placed individually under a 4 in. × 2 in. glass cylinder set in a glass petri dish of water. As the adults emerged they were transferred to a third insectarium with a controlled temperature of 80° F. and placed in netted cages measuring 2½ cu. ft. One cage contained fifty-one *atroparvus* females and two hundred *quadrimaculatus* males, and the second contained seventy *quadrimaculatus* females and one hundred and sixty *atroparvus* males. The mosquitoes were left together for a period of four to twelve days. As the males of each species died fresh specimens were added. A blood meal was given when necessary by inserting an arm inside the cage or by placing a rabbit in the cage overnight. A jar containing cotton-wool soaked in 10 per cent. dextrose was left in the cage during the day.

Between the fourth and twelfth days of the mosquitoes being together, seventeen females of the *atroparvus* female × *quadrimaculatus* male cross and nineteen females of the *quadrimaculatus* female × *atroparvus* male cross developed ripe ovaries. These females were caught and put separately into a glass cylinder set in a petri dish of water to lay their eggs.

Results and Observations.

(a) *atroparvus* female × *quadrimaculatus* male.

Number of females with developed ovaries	17
Number of females which laid one batch of eggs	17
Number of batches of eggs hatched	11
Number of females which laid two batches of eggs	6
Number of batches of eggs hatched	5
Number of females which laid three batches of eggs	1
Number of batches of eggs hatched	1

From the above statement it will be seen that seven batches of eggs failed to hatch. In each of the seventeen females the spermatheca was dissected, and only one proved negative. All the eggs appeared normal and showed characters of the female parent, and those which hatched did so within three days of being laid. The larvae were healthy and vigorous and the survival rate was high. One hundred and fifteen reached the pupa stage between eleven and sixteen days after hatching. Of the one hundred and fifteen pupae, twenty-six died.

The Adults.

From the eighty-nine pupae three female adults emerged normally and, although rather weak, lived for three to four days, but refused to feed on blood or dextrose solution. Forty-seven females emerged with great difficulty, their legs being entangled in their pupae cases, and thirty-nine females drowned while emerging. *Not a single male adult was seen.* Of the forty-seven females which emerged with great difficulty, all died within twenty-four hours.

(b) *quadrimaculatus* females × *atroparvus* males.

Number of females with developed ovaries	19
Number of females which laid one batch of eggs	19
Number of batches of eggs hatched	8
Number of females which laid two batches of eggs	19
Number of batches of eggs hatched	11
Number of females which laid three batches of eggs	13
Number of batches of eggs hatched	7
Number of females which laid four batches of eggs	5
Number of batches of eggs hatched	5
Number of females which laid five batches of eggs	2
Number of batches of eggs hatched	2
Number of females which laid six batches of eggs	2
Number of batches of eggs hatched.	2

From the above statement it will be seen that twenty-five batches of eggs failed to hatch, and that the first batches of eggs laid by three mosquitoes failed to hatch, whereas their second batches hatched normally. In each of the nineteen females the spermatheca was dissected and only two were negative. All the eggs appeared normal and showed the characters of the female parent, and those which hatched did so within three days of being laid. The larvae did not appear as healthy as those obtained from the *atroparvus* female × *quadrimaculatus* male cross and the survival rate was not high. Seventy-seven pupae developed between eleven and twenty-one days after hatching. Of the seventy-seven pupae, twenty-one died.

The Adults.

From the fifty-six pupae, nineteen female adults emerged normally. Six females emerged with difficulty and lived only a few hours, while thirty-four were unable to disentangle themselves from their pupae cases and seven were drowned in emerging. *Not a single male adult was seen.* Of the nineteen females which emerged normally, eleven took a human blood meal and two of these mosquitoes fed on blood four times over a period of nine days. The mosquitoes which fed on blood lived for four to nine days. All the nineteen females which emerged fed on dextrose solution.

The cross females which emerged normally refused to back-cross with either *atroparvus* or *quadrimaculatus* males.

DISCUSSION.

Although *A. quadrimaculatus* and *A. atroparvus* probably belong to the same group complex they are as widely separated as is *atroparvus* from *sacharovi.* The eggs of *quadrimaculatus* are quite distinct from those of *atroparvus* and the male adults are distinguishable from one another by the harpagos of the hypopygia. There are also bionomic differences, *quadrimaculatus* being much more anthropophilic than *atroparvus.* A fundamental difference of considerable interest is that *quadrimaculatus* was found to be susceptible to infection with a certain West African strain of *P. falciparum*, while *atroparvus* was completely refractory, at least under the conditions prevailing in our laboratory at the time of the experiment.

An attempt was made to ascertain why so many adults died during the act of emerging from their pupae cases. Emergence began in the usual way and generally the head, fore and mid-legs separated themselves from the pupae cases. Observations indicated that it is the hind pair of legs which obstruct emergence, for the claws appear to be embedded in the tissue of the pupa case.

It has been shown by several workers that some species of mosquito can be easily hybridized and that it is possible to raise successive generations of hybrids. Whether these results indicate that the original parents were not separate species we are not able to say.

Our results show that in nature these strains of *atroparvus* and *quadrimaculatus* could not fully develop a hybrid cross.

SUMMARY.

Hybridization took place under laboratory conditions between *Anopheles maculipennis* var. *atroparvus* Meigen and *Anopheles quadrimaculatus* Say.

Females of *A. maculipennis* var. *atroparvus* mated with males of *A. quadrimaculatus.*

The seventeen cross females produced, in all, seventeen batches of fertile eggs. Out of the seventeen females which laid eggs only one had a negative spermatheca. The larvae were healthy and vigorous and the survival rate was high. Only female adults emerged. All the females were weak and, with the exception of three, all had great difficulty in leaving their pupae cases. None were induced to feed on blood or dextrose solution.

Females of *A. quadrimaculatus* mated with males of *A. maculipennis* var. *atroparvus.*

The nineteen cross females produced, in all, thirty-five batches of fertile eggs. Out of the nineteen females which laid eggs two had negative spermathecae. Larval survival was not high. Only female adults emerged. Nineteen female adults emerged normally, eleven took a human blood meal and two of these mosquitoes fed on blood four times over a period of nine days. All the adults which emerged normally fed on dextrose solution. Efforts to back-cross these females with either *atroparvus* or *quadrimaculatus* males failed.

BOOK NOTICES.

Flies of the British Isles. By CHARLES N. COLYER and CYRIL O. HAMMOND. [Wayside and Woodland Series.] Sm. 8vo. London (Warne), 1951. Pp. 383, 48 col. pls., 55 half-tone pls., 15 text-figs. Price 30*s*.

This volume, by two Fellows of the Society, follows the familiar format of the Wayside and Woodland Series, but is much thicker than the average. It covers the whole Order Diptera down to family level, dividing it for the purpose into six Sections : Nematocera ; Brachycera ; Aschiza ; Calypterates ; Acalypterates and Pupipara. A key to the Sections is provided, and subsequently there are keys to the families in each Section.

Each family is given a diagnosis in fairly simple terms, followed by its habitat, biology, and what is known of its early stages. The subfamilies are then treated in turn, with mention of the principal genera, and fuller accounts of representative species. While there are frequent references to details of structure, and diagnostic characters the text is written from a collector's standpoint, and emphasizes chiefly the habitat and biology of the living insect. An appendix (33 pp.) gives a great deal of first-hand experience of Collection, Preservation and Examination of Diptera, and there is a useful Glossary.

The text is divided into twenty-five chapters, each with a list of references to more detailed works of identification The illustrations are profuse and accurate, including coloured and black-and-white figures of whole insects, and many details of structure referred to in the text and keys.

Fragments of New Zealand Entomology. By G. V. HUDSON. 8vo. Wellington, N.Z. (privately published), 1950. Pp. 188, 20 pls. (17 col.). Price 60*s*.

Completed by the author before his death in 1946, and published posthumously, this is a collection of miscellaneous observations on New Zealand insects, some of them first published many years ago, and now reissued. The longer contributions are a full account of the natural history of the New Zealand Glow-worm (*Arachnocampa luminosa* Skuse, Diptera, MYCETOPHILIDAE) ; a review of the New Zealand cicadas ; and an essay on " Some aspects of modern methods in entomology," first published in 1929.

The last is a lament that the delightful hobby of entomology is being spoilt by " the increasing influence of the professional entomologist, whose ambitions more often centre on a successful and remunerative career than on a study of Natural History for its own sake." There is a list of seven " disabilities and limitations which the amateur entomologist is free from."

An appendix lists the entomological works of Mr. Hudson, and there are numerous examples of the coloured figures which he considered " . . . in at least nine cases out of ten . . . are all sufficient for purposes of instant identification."

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The principal Publications of the Royal Entomological Society are *Transactions* and *Proceedings.*

The **Transactions** form an annual volume, each paper in the volume being issued as a separate part. The parts are issued irregularly throughout the year.

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Papers offered for publication in the *Transactions* are considered by the Publication Committee of the Society, which meets usually in the months of May and November. In order that papers may be considered at these meetings it is necessary for the manuscript and drawings for illustrations to be in the hands of the Registrar fourteen days before the meeting of the Committee.

The Society is prepared to undertake the provision of a reasonable number of figures, in line or half-tone. Colour work is accepted only by special arrangement.

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Series C is issued before every General Meeting. It contains abstracts of communications to be made, together with the titles of papers accepted for publication in the *Transactions.*

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As from January, 1936, the journal *Stylops* is continued as *Proceedings Series B. Taxonomy*. Copies of volumes 1–4 are available at £1 16*s.* 0*d.* each, post free.

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Smith, A., 1936, New Species of COCCIDAE. *Proc. R. ent. Soc. Lond.* (B) **6**: 301–306. pl. 1.

——, 1936, New species of COCCIDAE. *Trans. R. ent. Soc. Lond.* **84** : 901–936.

Titles of periodicals cited are to be abbreviated in the manner indicated in the *World List of Scientific Periodicals, 2nd edition,* 1934.

Authors are entitled to receive 25 copies of their papers free of charge and may purchase additional copies provided that request be made before publication.

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1951

Wednesday, October 3
„ November 7
„ December 5

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